Dwarf elephants on Mediterranean islands: A natural experiment in parallel evolution

Volume 1 of 2

by

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I, Victoria Louise Herridge, confirm that the work presented in this thesis is my own.

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Abstract

Mediterranean dwarf elephants represent some of the most striking examples of phyletic body-size change observed in mammals and are emblematic of the 'island rule', where small mammals become larger and large mammals dwarf on islands. The repeated dwarfing of mainland elephant taxa (*Palaeoloxodon antiquus* and *Mammuthus meridionalis*) on Mediterranean islands provide a 'natural experiment' in parallel evolution, and a unique opportunity to investigate the causes, correlates and mechanisms of island evolution and body-size change. This thesis provides the first pan-Mediterranean study that incorporates taxonomic and allometric approaches to the evolution of dwarf elephants, establishing a framework for the investigation of parallel evolution and key morphological correlates of insular dwarfism.

I show that insular dwarfism has evolved independently in Mediterranean elephants at least six times, resulting in at least seven dwarf species. These species group into three, broad size-classes: 'small-sized' (*P. falconeri, P. cypriotes* and *M. creticus*), 'medium-sized' (*P. mnaidriensis* and *P. tiliensis*) and 'large-sized' (*Palaeoloxodon* sp. nov. and '*P. antiquus'* from Crete). Size-shape similarities between independent lineages from the east and central Mediterranean indicate that homoplasy is likely among similar-sized taxa, with implications for the existence of meta-taxa. These homoplasies appear to result from the exploitation of ontogenetic trajectories common to the Elephantidae, underpinning the evolution of small size. Interspecific allometry between dwarf and full-sized species can be seen to result from these common, but grade-shifted ontogenetic trajectories, and this may also be true of broader macroevolutionary trends in the Proboscidea. These size-related grade-shifts suggest that similar, but increasingly extreme, modifications of pre-natal development underpin the evolution of insular dwarfism in elephants. By incorporating research into the morphology and ontogeny of teeth and post-crania in full-sized extant and extinct elephants, this thesis provides new insights into insular dwarfism, elephant systematics and elephant functional morphology and adaptation.

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Svetalana Nikolaeva (International Commission of Zoological Nomenclature) dealt patiently with my queries over various articles of the Zoological Code, and showed me the value of a dispassionate approach to taxonomy. Isabel McMann (Radcliffe Science Library, Oxford University) tracked down the minutes of the British Association meetings from 1862, and went through them on my behalf to see if any record remained of Hugh Falconer's paper presented on *'Elephas' melitensis*. Their help was fundamental to the outcome of my taxonomic revision of dwarf elephants.

Discussions with Eleanor Weston, William Parr, Charlotte Miller, Marco Ferretti, Kirsty Penkman and Wendy Dirks helped to improve the quality and scope of this thesis. Finally, an enormous thank-you must go to all of my friends and family, but especially to my husband, Adrian Glover. Without his unwavering support – emotional and technical – this thesis would not have been completed.

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Chapter 1: Introduction

The dwarf elephants of the Mediterranean islands represent some of the most striking examples of phyletic body-size change observed in mammals. They are also emblematic of the 'island rule' (Van Valen 1973), an ecotypic rule that has experienced a resurgence of research interest following the discovery of *Homo floresiensis*, a putative insular dwarf hominin (Brown *et al.* 2004). Mediterranean dwarf elephants have great popular appeal and are commonly mentioned within the first few paragraphs of papers examining the island rule, or insular dwarfism, even if they are not themselves the subject of those studies (e.g. Heaney 1978, Lister 1989, Meiri *et al.* 2006, Millien 2006). Despite this, their origins, systematics and evolution remain controversial (e.g. Palombo 2003, Poulakis et al 2006, Ferretti 2008). In this thesis I aim to redress this imbalance.

Here, I begin with a short history of dwarf elephant research, and then contextualise this within the island biology paradigm. I go on to explain the structure and broad aims of my thesis (in-depth literature reviews and detailed hypotheses related to these aims follow in subsequent chapters). This thesis is not an investigation into the causes of insular dwarfism. Instead I focus on core, baseline work into systematics and evolutionary process. However, understanding the importance of dwarf elephants within this wider research context explains why my research is necessary, pertinent and timely, as well as interesting in its own right.

1.1. Dwarf elephants and island biology

1.1.1. One hundred and fifty years of dwarf elephant research

The existence of dwarf elephants in the Mediterranean was first widely recognised during the mid-19th century, following the extensive collecting activities of Admiral (then Captain) Joseph Spratt and Dr. Andrew Leith Adams, both keen naturalists, on Malta (Spratt 1867, Adams 1870). Prior to this, the fossil faunas of the Mediterranean islands were little studied, and more often the subject of local folklore and myth, or accorded a religious significance (to this day fossil hippo and elephant remains are used as votive offerings at Christian shrines in Cyprus, although the practice is dying out, pers. obs.). In fact, the Cyclops myth may owe its origins to the dwarf elephant material of Sicily (elephant skulls, like the Cyclops, being characterised by tusks and a large, centrally positioned aperture in a relatively flattened face; this is the nasal opening, but could easily be mistaken for an eye by analogy with the anteriorly positioned orbits of humans) (Mayor 2001).

The first recorded discovery of Mediterranean dwarf elephants occurred in 1860, near to the town of Zebbug, central Malta (Spratt 1867). A sediment-filled cavern, 'excavated' by workmen in 1859 during the digging of a water-tank in the garden of Signor Buttegieg, yielded a molar which Buttegieg later presented to the Malta Library Museum (Spratt 1867, Falconer 1868). Spratt, prompted by this

molar, sifted through the 'accumulated heap of soil and fragments' that remained, apparently undisturbed, on the Buttegieg property, and obtained permission to investigate the cavern either side of the water-tank (Spratt 1867, p.288). Spratt's work yielded a large collection of elephant molars (as well as giant dormice, giant swan and giant tortoise) which he sent to Hugh Falconer in London. This material formed the basis for Falconer's presentation to the British Association in 1862, on a new species of 'pigmy' elephant '*Elephas' melitensis* (Anonymous 1862, Spratt 1867), the first unequivocal scientific reference to a Mediterranean dwarf elephant.[1]

By the early 20th century, a flurry of geological exploration across the Mediterranean had resulted in the description of six species of dwarf elephant: '*Elephas' melitensis* Falconer, in Busk 1867, '*E.' falconeri* Busk 1867 and '*E.' mnaidriensis* Adams 1874 on Malta and Sicily; '*E.' lamamorae* Major 1883 on Sardinia; '*E.' cypriotes* Bate 1903 on Cyprus and '*E.' creticus* Bate 1907 on Crete. At the same time, and well in to the 20th century, large fossil assemblages from Sicily were excavated and attributed to the various Maltese taxa (Pohlig 1891, Vaufrey 1929, Ambrosetti 1968). By the early 21st century, a further three taxa had been described from the Eastern Mediterranean, bringing the total number of Mediterranean dwarf elephants to nine: '*Loxodonta' creutzburgi* Kuss 1965 and *'E.' chaniensis* Symeonidis *et al.* 2000 on Crete, and '*E.' tiliensis* Theodorou *et al.* 2007 on Tilos (a small island near to Rhodes, in the Dodecanese). Numerous unidentified elephant fossils are also known from the Greek islands of Delos, Naxos, Kynthos, Serifos, Melos and Rhodes (Palombo 2001a), and, if each of these is a separate island endemic, the number of Mediterranaen dwarf elephant species could be as high as fifteen. Thus, although the taxonomy, synonymy and generic attribution of Mediterranean elephants is the subject of ongoing debate (reviewed in Chapter 4), there is overwhelming evidence that dwarfing occurred multiple times, and to different degrees (e.g. Figure 1.1), in Mediterranean Pleistocene elephants.

Dwarf elephants and elephantoids also make up a major component of Pleistocene (and Miocene, in the case of some Japanese fossils; Saegusa 2008) insular faunas outside of the Mediterranean. Dwarf or 'small-sized' mammoths are known from the Californian Channel Islands (*M. exilis;* Roth 1982), and from Wrangel Island (off the coast of Siberia; Lister 1996a); while dwarf stegodons (part of an extinct clade of proboscideans which form the sister-group to the Elephantidae; Shoshani 1998) have been found on islands in the Indonesian archipelago (Van den Bergh 1999) and Japan (Sondaar & Van den Geer 2005, Saegusa 2008). Dwarf elephants are thus a wide-spread Pleistocene phenomenon and they are not the only Pleistocene insular taxa to be characterised by body-size change. Dwarf hippopotamus, dwarf deer, giant rodents and giant swans are well known components of Mediterranean island faunas, often found in association with dwarf elephants (Adams 1874, Marra 2005). Similarly, the fossil faunas contemporaneous with dwarf stegodons in Indonesia include giant rodents, giant komodo dragons and, controversially, a dwarf hominin (Van den Bergh 1999, Brown *et al.* 2004, Sondaar & Van der Geer

[1] There is an earlier reference to a molar from Gozo, identified by Hugh Falconer as *'Elephas primigenius'* (Smith 1847), which may belong to a dwarf taxon. This cannot be verified as the specimen cannot be located in Maltese or British museum collections (Michael Gatt, pers. comm 2009); Falconer's memoirs indicate that he was wary of assigning 'pigmy' status to elephant teeth unless he could be sure they were not milk-teeth (Falconer 1868, p. 292).

Figure 1.1. Size variation in Mediterranean dwarf elephants. *Palaeoloxodon antiquus*, the probable ancestor of a number of Mediterranean dwarf elephants, became dwarfed to differing degrees on different islands. Shown here are tibiae of (from left to right) 'female' and 'male' morphotypes of (i) *P. falconeri*, a 'small-sized' dwarf elephant from Spinagallo Cave, Sicily, and (ii) *P. tiliensis*, a 'medium-sized' dwarf elephant from Charkadio Cave, Tilos. Inset: the author holding a juvenile/sub-adult tibia of *P. antiquus* from Aveley, Essex (left; note the unfused proximal epiphyseal line, and the unfused and missing distal epiphysis), and an adult 'female' tibia from Spinagallo Cave (right). Photo credits: the author and Adrian Glover.

2005). These size-change trends are now understood to part of a wider phenomenon related to evolution on islands.

1.1.2. Islands and evolutionary biology

Charles Darwin's observations on the mockingbirds of the Galápagos archipelago highlight the importance of islands in the development of evolutionary theory (Darwin 1837, Figure 1.2). It was not until the latter half of the 20th century, however, that islands took centre stage in discussions on speciation (Mayr 1963; Kadmon &Pulliam 1993), adaptive radiation (Losos *et al.* 1998, Schulter 2000), population dynamics (Cantrell *et al.* 1996, Morrison 2002), biogeography (MacArthur & Wilson 1967, Case & Cody 1987, Lomolino 2000) and conservation (Diamond 1976, Boecklen & Gotelli 1984, Hanski 1999). Islands are characterized by a suite of features that are both interesting in their own right and make them ideal for the study of ecological and evolutionary processes (MacArthur & Wilson 1967, Case 1978). Compared to an equivalent area of continent or ocean, islands are relatively simple objects for study, being discrete entities of land that can be delimited and measured with little ambiguity and are, with respect to the mainland, depauperate in fauna and flora (MacArthur & Wilson 1967). Immigration and emigration to and from islands is low, for terrestrial species at least, and islands commonly have more equable climates than the mainland (MacArthur & Wilson 1967, Marra 2005). Owing to niche availability and thus the capacity for adaptive radiations, islands are often 'hot spots' for biodiversity, with high levels of endemism (Myers *et al*. 2000, Cardillo *et al.* 2006). Evolutionary rates have also been shown to be higher on islands (Millien 2006), and their multiplicity provides 'replicates' of natural 'experiments' for the testing of evolutionary and ecological hypotheses (MacArthur &Wilson 1967).

Despite the recognition of Mediterranean dwarf elephants as an insular phenomenon, it took over 100 years before the island environment itself was proposed as a causal factor in their evolution (Ambrosetti 1968, Sondaar 1977). Early publications focussed instead on dwarf elephant taxonomy, although Adams (1870) suggested that insularity caused the extinction of Maltese and Sicilian large mammal faunas (thus implying they originally existed in a non-insular environment). This time-lag is similar to that observed between Darwin's observations and the beginnings of the island biology paradigm. Both probably reflect broader intellectual trends in biological research, which became more interested in mechanism and adaptation after the 'Modern Synthesis', and the influence of MacArthur and Wilson's (1967) theory of island biogeography. At the same time, in palaeontology, a better understanding of plate tectonics, geological time and past climatic changes supported the idea that Sicily, Malta, Crete and Cyprus were islands for much of the Pleistocene, and that dwarf elephants and their contemporaries were indeed an island fauna. The extension of neontological research into the unique features of island faunas and floras to extinct taxa was a logical step. First, the insular size-trends seen in Mediterranean elephants and other fossil taxa were seen to exemplify (and take to extremes) the 'island rule' (e.g. Sondaar 1977, Heaney 1978, Lister 1989), and second, the parallel evolution of dwarf elephants on islands throughout the Pleistocene could be treated as a natural experiment in parallel evolution (Sondaar 1977, Roth 1992a).

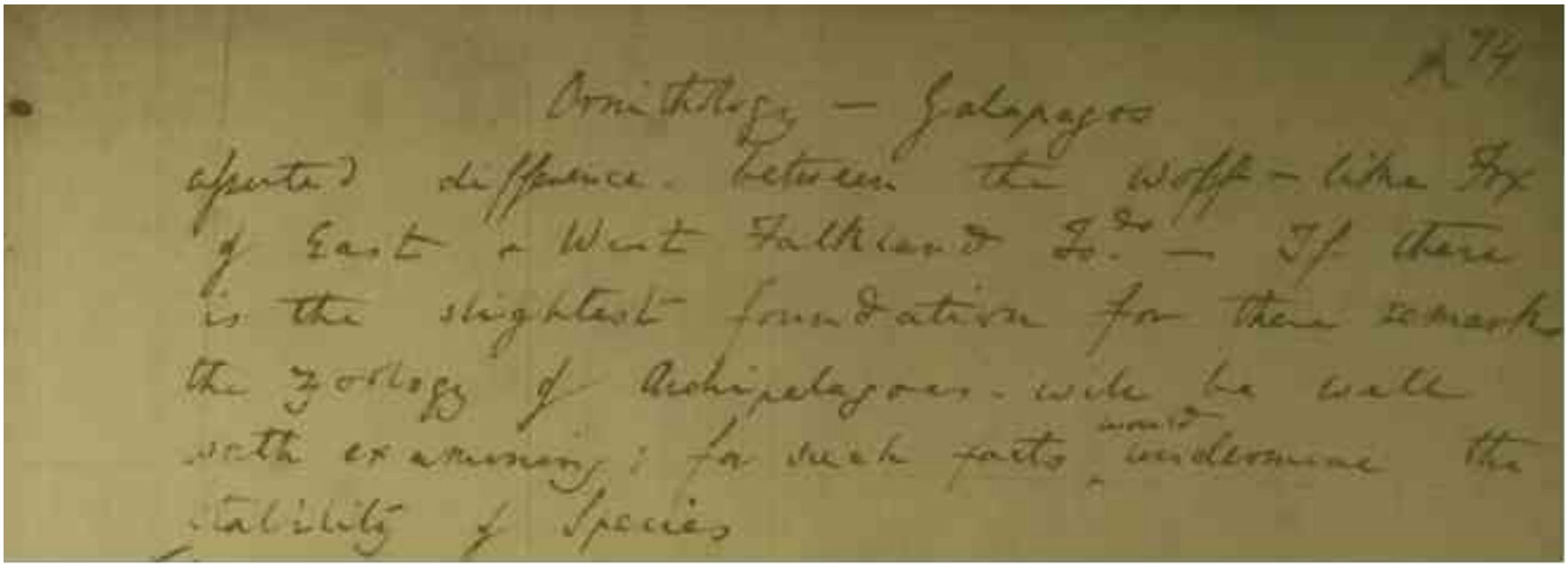

Figure 1.2. Excerpt from the manuscript of *Ornithological Notes* by Charles Darwin (1837). Referring to the possibility that the Galapagos mockingbirds were different species (rather than merely 'varieties') to each other, and to the mainland mockingbirds, Darwin writes "If there is the slightest foundation for these remarks the zoology of archipelagos will be well worth examining; for such facts would undermine the stability of species." Source: http://darwin-online.org

1.1.3. The island rule

Foster (1963, 1964) first established that the occurrence of gigantism in insular rodents, and dwarfism in insular lagomorphs and artiodactyls, was specifically linked with the island environment. This trend was summarised in broader terms by Van Valen (1973) as the 'island rule': on islands, small mammals typically evolve larger body-size, while large mammals dwarf (Figure 1.3). The island rule has had overwhelming support from subsequent studies, carried out on islands throughout the world (e.g. Sondaar 1977, Case 1978, Heaney 1978, Angerbjorn 1985, Lomolino 1985, Clegg & Owen 2002, Lomolino 2005). Some taxa, however, do not seem to adhere to the island rule – there are equivocal results for marsupials, carnivores and some lagomorphs (Lawlor 1982, Meiri *et al*. 2004), and there is seemingly no trend in insectivorous rodents (Case 1978) – and its generality has been questioned (Meiri *et al.* 2006, 2008). Nevertheless, the island rule is widely accepted and is still considered as having 'fewer exceptions than any other ecotypic rule in animals' (Van Valen 1973, p.35; Lomolino 2005, Lomolino *et al.* 2006). Elephants are certainly not 'exceptions to the rule'; they are unequivocally a 'large mammal' as the end-member of the mainland mammalian body-size spectrum, and are also the most extreme example of insular body-size reduction (the ca. 10,000 kg *P. antiquus* dwarfing to the ca. 100 kg *P. falconeri* on Sicily; Roth 1990, Figure 1.1).

1.1.4. Causes of insular body-size change

The factors that influence body-size change on islands have been debated extensively over the last 40 years. The appeal of finding a universal explanation to a seemingly universal phenomenon is understandable, but attempts to reconcile the ecology and biology of insular faunas and their differing body-size changes into a single, predictive theory have not succeeded. Instead a number of theories have been proposed, invoking island area (Foster 1964, Heaney 1978), distance from the mainland (Foster 1964), resource limitation (Sondaar 1977, Case 1978; Angerbjorn 1985, Lomolino 1985, Lawlor 1982, Roth 1992a, Millien & Damuth 2004), competitive release (Case 1978, Heaney 1978, Angerbjorn 1985, Lomolino 1985, Raia & Meiri 2006), predation pressure (Case 1978, Angerbjorn 1985, Lomolino 1985, Lawlor 1982, Raia & Meiri 2006), territoriality (Case 1978), immigrant selection (Lawlor 1982, Lomolino 1985), feeding niche (Lawlor 1982, Raia *et al.* 2003) and life history traits (Bromage *et al.* 2002, Raia *et al.* 2003).

These hypotheses differ mostly in the relative weight they give to the factors thought to cause body size change, rather than being mutually exclusive, and can be crudely subdivided into those which see the insular environment as 'permissive' (enabling evolution towards an 'optimal' body size denied by the organism's mainland niche) or 'restrictive' (a more hostile insular environment requiring body-size change) (Table 1.1). The theoretical 'optimal' body-size of an organism is that which maximises energy acquisition, reflecting the energetic trade-off between resource provisioning, growth and reproduction (Damuth 1993). It is hypothesized as either 100 g (Brown *et al.* 1993) or 1 kg (Damuth 1993) in

Cause/Correlate	Permissive or Restrictive?	Size Trend		Island Biogeography
		Small	Large	
competitive release	Permissive	**gigantism**	**dwarfism**	co-vary with island area and/or distance from mainland
predation pressure	Permissive	gigantism?	**dwarfism**	
territoriality	Permissive	gigantism	dwarfism	
resource limitation	Restrictive	dwarfism*	**dwarfism**	
feeding niche	Permissive for generalists	gigantism	dwarfism	
	Restrictive for specialists	dwarfism	**prey-size tracking**	
life history	Permissive	gigantism	**dwarfism**	N/A**
immigrant selection	-	**gigantism**	?	N/A***

Table 1.1. Causes and correlates of insular body-size change. A number of explanations have been hypothesized for island body-size trends, and these can be considered as 'permissive' if the island environment releases an organism from a body-size constraint imposed by its mainland niche, or 'restrictive' if insularity itself imposes a new constraint. Hypotheses are categorized, alongside their expected affect on 'small' and 'large' vertebrates (as defined relative to an 'optimal' size), and expected co-variance owing to the tenets of island biogeography. Hypotheses believed to have greater importance are highlighted in bold (after Heaney 1978, Lomolino 1985, Raia & Meiri 2006); these vary for small and large mammals owing to the 'relative nature' of island area. * fasting ability may select for gigantism in resource limited situations, particularly in small mammals. ** secondarily affected as 'optimum size' is determined by ecological/environmental correlates that co-vary with island biogeographic parameters. *** distance from mainland will affect patterns of island diversity (e.g. selecting against bad colonisers), which may themselves impact on selection pressures. References in text.

mammals, and the island rule is often taken as evidence in support of this concept, as island species seem to be evolving towards an intermediate size (Meiri *et al.* 2005, Figure 1.3b). However, on islands, as on the mainland, competition, resource availability and niche incumbency will result in adaptive sub-optima at which organisms will reach an evolutionarily stable state (Raia & Meiri 2006). This stresses the distinction between 'direction' and 'magnitude' of size change on islands when investigating the causes and correlates of the island rule. The island rule expresses patterns of directionality, while most investigations seek to understand these patterns through exploration of the magnitude of size change (e.g. Figure 1.3b).

1.1.5. Causes of insular dwarfism in elephants

Of the various potential causes and correlates, dwarfing in elephants has been specifically linked with resource limitation (owing to smaller island areas relative to the mainland; e.g. Sondaar 1977, Heaney 1978, Roth 1992a, Lister 1996a), release from predation and inter-specific competition (Sondaar 1977, Raia & Meiri 2006), and with the adaptive value of size-correlated life history effects (Bromage *et al*. 2002, Raia *et al.* 2003). Support for these hypothesis is limited and/or equivocal. Although no study has tested the relationship between island area and degree of dwarfism in elephants, following the size categories of Vaufrey (1929) and Palombo (2001a) at least two differently-sized taxa are recognised on Sicily, on Malta and on Crete (Palombo 2001a, Poulakakis *et al.* 2002a, Marra 2005), and possibly also on Cyprus (Reese 1995), belying any simple relationship.

Competition and predation levels also provide equivocal support for observed dwarfing patterns. On Sicily, small-sized elephants had no predators and no herbivorous competitors, while the larger dwarf elephants of a later fauna are found alongside hippopotamus, deer, hyaena and lion (Bonfiglio *et al*. 2002, Marra 2005), consistent with the hypothesis that release from either of these factors promotes dwarfism in large herbivores (Raia & Meiri 2006). There is no evidence for carnivores in any of the elephant faunas on Crete, but the larger-sized *P. antiquus creutzburgi* from Crete is believed to be contemporaneous with dwarf hippopotamus and dwarf deer, whereas the smaller-sized *M. creticus* is thought to have had no herbivorous competitors. This supports Raia & Meiri's (2006) suggestion that competitive release is a more important driver of insular dwarfism than lack of predation. Yet the 'small-sized' dwarf elephants of Cyprus (considered equivalent in size to *P. falconeri*; Davies & Lister 2001) are contemporaneous with dwarf hippopotamus (Bate 1904, Simmons 1989, Reese 1995), even if competition between these taxa is far from certain.

Selection for small body-size as an adaptation to a 'faster' life history provides a potential common framework for dwarfism in elephants, but does not explain differences in the degree of dwarfism observed. In fact, all evidence in support of this hypothesis comes from the two smallest dwarf taxa (after Vaufrey 1929: *P. cypriotes* and *P. falconeri*). A faster life history has been inferred from (i) incremental growth-line evidence in *P. cypriotes* tooth enamel, either via growth truncation (Bromage *et al.* 2002) or increasing developmental rates (Bromage *et al.* 2009), and (ii) apparent high rates of fecundity and

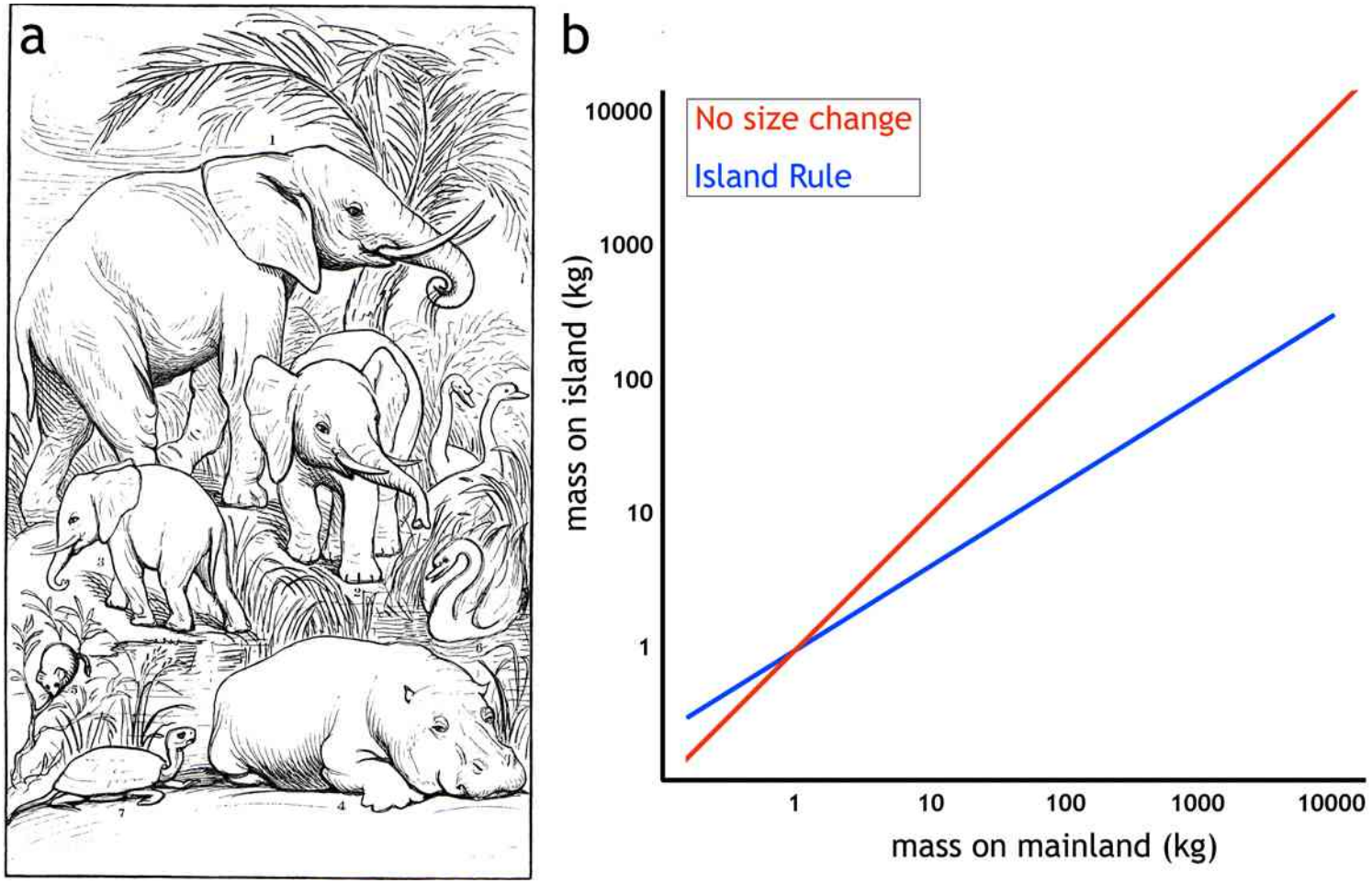

Figure 1.3. The island rule. On islands, large mammals often become dwarfed while small mammals evolve larger body sizes. **a. I**n the Pleistocene of Europe this phenomenon is often observed, with island faunas characterised by dwarf elephants, dwarf hippos and giant rodents, alongside giant swans and giant tortoises (image from Adams 1870). **b.** This trend can be tested for by regression analysis of mass/size of island species against the mass/size of their mainland sister-taxa: a slope <1.0 is consistent with the island rule (blue). The point at which this line crosses the theoretical log-linear regression line for mass on mainland = mass on island (slope =1.0; red line) indicates the size which (i) delineates 'small' from 'large' organisms, (ii) indicates the size at which no size change is expected on islands and (ii) is by many interpreted as the 'optimal' body size that other taxa are evolving towards (Damuth 1993, Meiri *et al*. 2005). Here I have placed this cross-over point at 1 kg, in line with Damuth's (1993) optimum size for mammals, although 100 g and 250 g have also been suggested (Maurer *et al*. 1992, Brown *et al*. 1993).

juvenile mortality in *P. falconeri* (Raia *et al*. 2003). There are, however, some issues with the analysis of Raia *et al*., as high mortality rates and high fecundity are inferred from the same assemblage age-profile. Life-history parameters for other, larger-sized dwarf taxa have been inferred only from mammalian interspecific allometry (Roth 1992a), and need to be supported by independent data before this hypothesis can be considered to have broad support from comparative studies.

1.1.6. Islands as 'natural experiments'

Causes of insular body-size change in elephants therefore remain in the realm of plausible, but not thoroughly substantiated, hypotheses. In this respect they are typical of the broader discussions surrounding the island rule. Correlations between proposed causal factors and the magnitude of size change appear to be weak or non-existent, and no one hypothesis clearly outcompetes the rest. If one considers the broader framework of island biogeography, such ambiguity is unsurprising because island area (and thus resource limitation) and species diversity (and thus competition and predation) are expected to covary (MacArthur & Wilson 1967; Table 1.1). Rates of immigration, dependent on degree of isolation, will also covary with species diversity, providing an additional co-factor (MacArthur & Wilson 1967). Together with the – essentially stochastic – colonisation history which determines niche incumbency, this means that no two islands are likely to be identical.

Islands are thus unlikely to be 'true' replicates in terms of their ecology, and anything other than a weak and imprecise macroevolutionary trend would be unusual, especially when sample sizes are small (as they often are when considering a single taxon). Any additional ambiguity over the number and body-size of insular taxa, or in the reconstruction of the island environment, will introduce further error, and potentially obscure trends. This last point is highly pertinent to dwarf elephant research. First, no in-depth, pan-Mediterranean revision of dwarf elephant systematics has been made since Osborn (1942). Second, there has been no comprehensive, comparative study of body-size differences across the various Mediterranean dwarf taxa. Third, the geochronology of Mediterranean dwarf elephants (and their associated faunas) has received little critical attention, and has been heavily reliant on discredited amino acid racemization methods (Blackwell *et al.* 1990; Chapter 3). This has potential implications for published reconstructions of contemporaneous island taxa, and consequently competition and predation levels. Finally, in a tectonically active region such as the Mediterranean, present-day island area may not approximate that of the past. Mediterranean dwarf elephants therefore require careful, in-depth investigation if they are to serve as 'natural experiments' for investigating the ecological and environmental drivers of insular body-size change.

Dwarf elephants are important components of Pleistocene insular faunas, and have been cited as classic examples of island evolution (Millien 2006). They are treated as exemplars of the island rule (e.g. Heaney 1978, Lister 1989, Meiri *et al.* 2006, Benton *et al*. 2010); they are incorporated into meta-analyses investigating the tempo, mode and causes of island evolution (Millien 2006, Meiri *et al.* 2008); and their degree of endemism, inferred from qualitative assessments of size-reduction, has itself been

used to support the existence of a more insular environment (i.e. a smaller, more isolated island, Bonfiglio *et al*. 2002). Yet the foundation for these studies – our knowledge of the systematics, morphology and evolution of dwarf elephants – is weak. This thesis addresses a series of broad and inter-connected questions about the parallel evolution of Mediterranean dwarf elephants, aiming to strengthen these foundations and thereby to contribute a rigorous case study to the island dwarfing debate.

1.2. Aims and content of this thesis

This thesis does not set out to ask 'why' elephants became dwarfed on islands during the Pleistocene. Instead, its focus is on the systematics and evolution of these emblematic taxa. In the broadest sense, I attempt to find answers to some basic questions: when and where did Mediterranean elephants evolve? How many times did they evolve? Who were their mainland ancestors? What did they look like? What mechanisms drove this evolution? Each of these questions can be broken down into a number of hypotheses, outlined in more detail in the relevant chapters, that are informed by a wide range of palaeontological and evolutionary theory summarized in literature reviews within each chapter. In consequence, the four main research chapters (Chapters 3 to 6) are thematically distinct, and largely self-contained. Nevertheless, these chapters are mutually informative, and form a single body of research that leads to a more complete picture of the diversity and evolution of Mediterranean dwarf elephants. Over the next six chapters, I establish what we can – and cannot – say about when, where and how Mediterranean dwarf elephant species evolved. Below, I summarize the key questions addressed in each chapter; these are discussed fully in the relevant chapters.

Chapter 2: Materials and Methods

This chapter introduces materials and methods that are common to all chapters (measurement protocols and collections information). More detailed methodologies, including data analysis, can be found in the methods sections of subsequent chapters.

Chapter 3: Palaeogeography and Geochronology

Here I critically review the geochronological and palaeogeographical evidence for dwarf elephant evolution to establish the limits of our current knowledge. I ask the following questions:

- Were all target islands isolated from one another in the past?
- How confident can we be that modern day island area approximates past island area?
- What methods are the basis for the existing dwarf elephant geochronology?
- How reliable are those methods?

The answers to these questions enable me then to ask:

- Can we identify which dwarf elephant samples/localities are temporally and/or geographically distinct?

Answering this last question provides a contextual framework for dwarf elephant taxonomy (Chapter 4), using contemporaneity and sympatry as primary hypotheses of conspecifity. This chapter also establishes if we have sufficiently reliable palaeoenvironmental and geochronological information to address questions relating to the causes and rate of insular evolution.

Chapter 4: Systematics

This chapter addresses dwarf elephant nomenclature, taxonomy and systematics, and is concerned with the identity and taxonomic integrity of dwarf elephant fossil material. I ask the following questions:

- Are the existing dwarf taxa valid, and consistent, for each island, with a single species hypothesis?
- How many dwarf elephant species are there?
- How many independent dwarfing events were there? (This is not necessarily equivalent to the number of taxa)
- What is the impact of size-related homoplasy on dwarf elephant systematics?
- To which genus does each dwarf taxon belong?
- What is the likely mainland sister-taxon of each dwarf elephant species?

I thus produce a revised taxonomic framework for Mediterranean dwarf elephants, and a summary of the morphological similarities and differences between these taxa. This new taxonomy underpins the division and interpretation of dwarf elephant data in Chapters 5 and 6. It also establishes which taxa have dwarfed to similar degrees, enabling better use of dwarf elephants in more general discussions of the island rule.

Chapter 5: Ontogeny

Because insular dwarfing is thought to involve an ontogenetic mechanism, understanding how elephants (extant and extinct) grow or grew is essential for not only deciphering the evolutionary pattern, but also distinguishing dwarfs from juvenile taxa and strengthening age assessments. Here I investigate epiphyseal fusion, and its relationship with limb-bone growth and ontogeny in full-sized elephants. I ask:

- Are epiphyseal fusion patterns similar across the Elephantidae (including Mediterranean dwarfs)?
- How variable are patterns of epiphyseal fusion intraspecifically?

- Are rates of limb-bone growth similar, between bones and between species, in full-sized elephants?
- Does epiphyseal fusion coincide with the end of longitudinal growth?

By answering these questions I aim to identify possible heterochrony in fusion sequences between full-sized and dwarf elephants, that might provide insight into their evolution and/or morphological differences, and obtain insights into absolute rates of limb-bone growth in extant taxa that help to inform the relative growth rates investigated in Chapter 6. This chapter also establishes the developmental equivalence of bones at different stages of fusion; in doing so it underpins how I identify 'adult' limb-bone specimens in Chapter 4 and Chapter 6.

Chapter 6: Allometry

One of the most obvious questions that dwarf elephants raise is, "what were the functional consequences of extreme size reduction, given that gravity should be a major constraint on the biology of large ancestral elephants but presumably less so in descendants ~10% their size?". Chapter 6 extends the research into size-related trends identified in Chapter 4, and the ontogenetic trends identified in Chapter 5, by considering molar and limb-bone allometry in dwarf and full-sized elephants. I ask:

- Is there evidence of inter- and intraspecific allometry in dwarf and full-sized elephants?
- Is ontogenetic allometry similar across elephant species, including dwarf taxa?
- If so, can interspecific allometry (and thus dwarf elephant adult morphology) be 'explained' by ontogenetic scaling?
- Is inter- and intraspecific allometry consistent with functional scaling hypotheses?

In addressing these questions, I aim to establish if the evolution of insular dwarfism exploited similar developmental mechanisms in each dwarf taxon, and is thus consistent with 'true' parallel evolution. I also aim to integrate ontogenetic and biomechanical approaches to scaling studies, to see if together they can shed new light on dwarf elephant adaptation, and elephant functional morphology in general.

Chapter 7: Conclusion

Finally, in Chapter 7, I bring the findings of Chapters 3 to 6 together, and summarise their implications for our understanding of dwarf elephants, the wider phenomenon of insular dwarfism, and elephant evolution. In doing so, I aim to contextualise my contributions to these fields and to make clear proposals for the direction of future research.

Chapter 2: Material and Methods

This chapter describes the materials and methods which are common to subsequent chapters: the fossil and comparative collections studied for this thesis and the measurement protocols used to study them. Detailed methodological information, including statistical methods and my hypothesis-testing approach, are provided on a chapter-by-chapter basis as they are specific to each chapter's aims.

2.1. Fossil and comparative collections

Mediterranean dwarf elephant fossils have been a focus of research interest since the mid-19th Century, and their remains form part of palaeontological collections the world over. These collections form the basis of my research. Time and funding constraints prevented an exhaustive survey of the fossil material, and instead I focussed on the large, historically important collections of dwarf elephant dental and postcranial material in London, Sicily, Malta and Athens (Table 2.1). These collections include dwarf elephant specimens from the Eastern and Western Mediterranean basins, cover the full stratigraphic and body-size range of Mediterranean elephants, and include type-material for *Palaeoloxodon falconeri*, *P. melitensis, P. mnaidriensis, 'Elephas' creticus*, *P. cypriotes* and *P .tiliensis* (the types of *P. chaniensis*, *P. creutzburgi* and *Mammuthus lamarmorae* were not available for study). Section 3.1 discusses how my choice of collections affects the evolutionary and systematic hypotheses that can be tested. The taxonomy and nomenclatural history of the dwarf elephant taxa included in this study are discussed in Chapter 4, while fossil locality information can be found in Appendix 1.

Full-sized elephant material was also studied, for comparison with dwarf species (Table 2.2). *P. antiquus* (widely considered to be the mainland ancestral taxon for Mediterranean dwarf elephants; see Chapter 4) material from the UK and Germany forms the core of my full-sized elephant molar sample, and the basis for my taxonomic revision of dwarf elephants. Molar data is supplemented by literature data for *P. iolensis* and *Loxodonta atlantica* (Maglio 1973) and for *E. maximus*, *L. africana* and *M. primigenius* (Roth 1992a), and by the unpublished data of A. Lister and H. Van Essen for *M. meridionalis*.

Postcranial material for full-sized elephants is less common in museum collections. Post-cranial bones are heavy and unwieldy (especially in fossil form), require large amounts of storage space and specialist curatorial assistance for access, and have limited taxonomic usefulness. In consequence, the material available for study was limited. Again, to maximise use of time and financial resources, I focussed on the large comparative zoology collections at the Natural History Museum, London and the Afrika Museum, Tervuren, Belgium (formerly known as the Royal Museum of Central Africa) for extant elephant material (Table 2.2). The extant elephants *E. maximus* and *L. africana* phylogenetically bracket the Elephantidae, and their morphology can be directly linked with experimental data on locomotion and biomechanics, as well as body-mass estimation studies. As such, they form an ideal study-sample for

Collection	Abbreviation	Fossil Locality		Species
		Site	Island	
Athens University	AU	Charkadio Cave	Tilos	*E. tiliensis*
Natural History Museum, Heraklion, Crete	NHM Crete	Katharo Basin	Crete	*E. antiquus creutzburgi*
Natural History Museum, London	NHM	East Crete	Crete	*E. antiquus*
		Cape Maleka	Crete	*E. creticus*
		Imbohary	Cyprus	*E. cypriotes*
		Zebbug Cave	Malta	*E. falconeri*, *E. melitensis*
		Mnaidra Gap	Malta	*E. falconeri?*, *E. melitensis*, *E. mnaidriensis*
		Gandia Fissure	Malta	*E. mnaidriensis*
		Benghisa Gap	Malta	*E. falconeri?*, *E. melitensis*, *E. mnaidriensis*
		Unknown	Malta	*E. melitensis, E. mnaidriensis*
		Cavern di Carini	Sicily	Undescribed material
Ghar Dalam Museum	GD	Ghar Dalam Cave	Malta	*E. falconeri*, *E. melitensis*, *E. mnaidriensis*
Institut de Paléontologie Humaine, Paris	IPH	Luparello Cave	Sicily	*E. falconeri*, *E. melitensis*
Museo G. Gemellaro, Palermo, Sicily	GG	Luparello Cave	Sicily	*E. falconeri*
		Puntali Cave	Sicily	*E. mnaidriensis*
		Za Minica	Sicily	*E. mnaidriensis*
Messina University, Messina, Sicily	MU	San Teodoro Cave	Sicily	*E. mnaidriensis*
Natural History Museum, Milan	NHM (Milan)	Puntali Cave	Sicily	*E. mnaidriensis*
		Unknown	Sicily	*E. mnaidriensis*
Ferrara University, Ferrara	FU	Puntali Cave	Sicily	*E. mnaidriensis*
		Unknown	Sicily	*E. mnaidriensis*
Catania University, Catania, Sicily	CU	Spinagallo Cave	Sicily	*E. falconeri*

Table 2.1. Collections of dwarf elephant material used in this study. Species names follow the collections' attributions, taken from catalogues and/or label information. See Appendix 1 for site descriptions, and Chapter 4 for discussion of taxonomy and nomenclature.

Collection	Abbreviation	Species
Afrika Museum, Tervuren, Belgium	RMCA	*L. africana*
		E. maximus
Natural History Museum, London	NHM	*L. africana*
		E. maximus
		P. antiquus
University of Rome La Sapienza, Rome	URLS	*P. antiquus*
Berlin University, Berlin	BU	*P. antiquus*
Staatliches Museum für Naturkunde, Stuttgart	SMNS	*P. antiquus*
Hessichen Landesmuseum, Darmstadt	LMD	*P. antiquus*

Table 2.2. Collections of full-sized fossil and extant elephants used in this study.

investigating size constraints on limb bone morphology. The *P. antiquus* post-cranial sample was less extensive, and drawn from the UK, Germany and Italy (Table 2.2). Both the post-cranial and molar material for *P. antiquus* are therefore biased toward northern European specimens, and this must be borne in mind when interpreting the taxonomic importance of morphological differences with Mediterranean dwarf elephants.

2.2. Data collection protocols

2.2.1. Teeth

Elephant cheek-teeth are highly derived. They are molariform, large relative to the mandible and maxilla, and are replaced 'horizontally', rather than vertically, with developmentally younger, more mesial teeth wearing down vertically as they are also progressing forward through the jaw. At the same time, developmentally later teeth form distally to replace them, forming a continuous, 'conveyor belt'-like occlusal surface until the last (sixth) molar has been completely worn down (Figure 2.1; Maglio 1973, Roth 1982). Tooth development extends over much of the life of an elephant (upwards of 30 years in African elephants; Laws 1966), and this mechanism of replacement has been interpreted as an adaptive strategy for extending the lifespan of the dentition in a large, grazing mammal (Maglio 1972, 1973). The rate of tooth progression and wear is fairly constant within extant elephant species, and has enabled ageing schemes to be developed for *L. africana* (e.g. Laws 1966, Jachmann 1988) and *E. maximus* (Roth & Shoshani 1988) (see Chapter 5).

Each tooth is made up of a series of 'plates' or 'lamellae' (I use these terms interchangeably), which are dentine-filled pockets of enamel, bound together by cement. In a fully-developed tooth, the enamel of each plate joins to the next, producing a concertina-like enamel layer in mesiodistal cross-section, and forms a single unit. The anterior portion of a tooth may be erupted and in wear before the tooth is fully formed, and posterior plates may be loose within the tooth alveolus (Figure 2.1); together this means that, once isolated from the jaw, complete elephant teeth are rare. Despite this, molar morphology forms the basis of much of elephant taxonomy, including in this thesis (skull material was not used owing to ongoing research on this material by M. Ferretti and M. R. Palombo). Molar wear can provide taxonomically informative characters: once in occlusion, the enamel apex of each plate is worn down such that the occlusal surface comprises a series of enamel loops of 'figures', the shape and early wear-pattern of which are taxonomically informative (Figure 2.2; each enamel figure is a cross-section of the plate in the occlusal plane). I also follow the measurement protocols developed by Maglio (1973), with minor modifications, which allow for many of the peculiarities of elephant dentition and minimise measurement error.

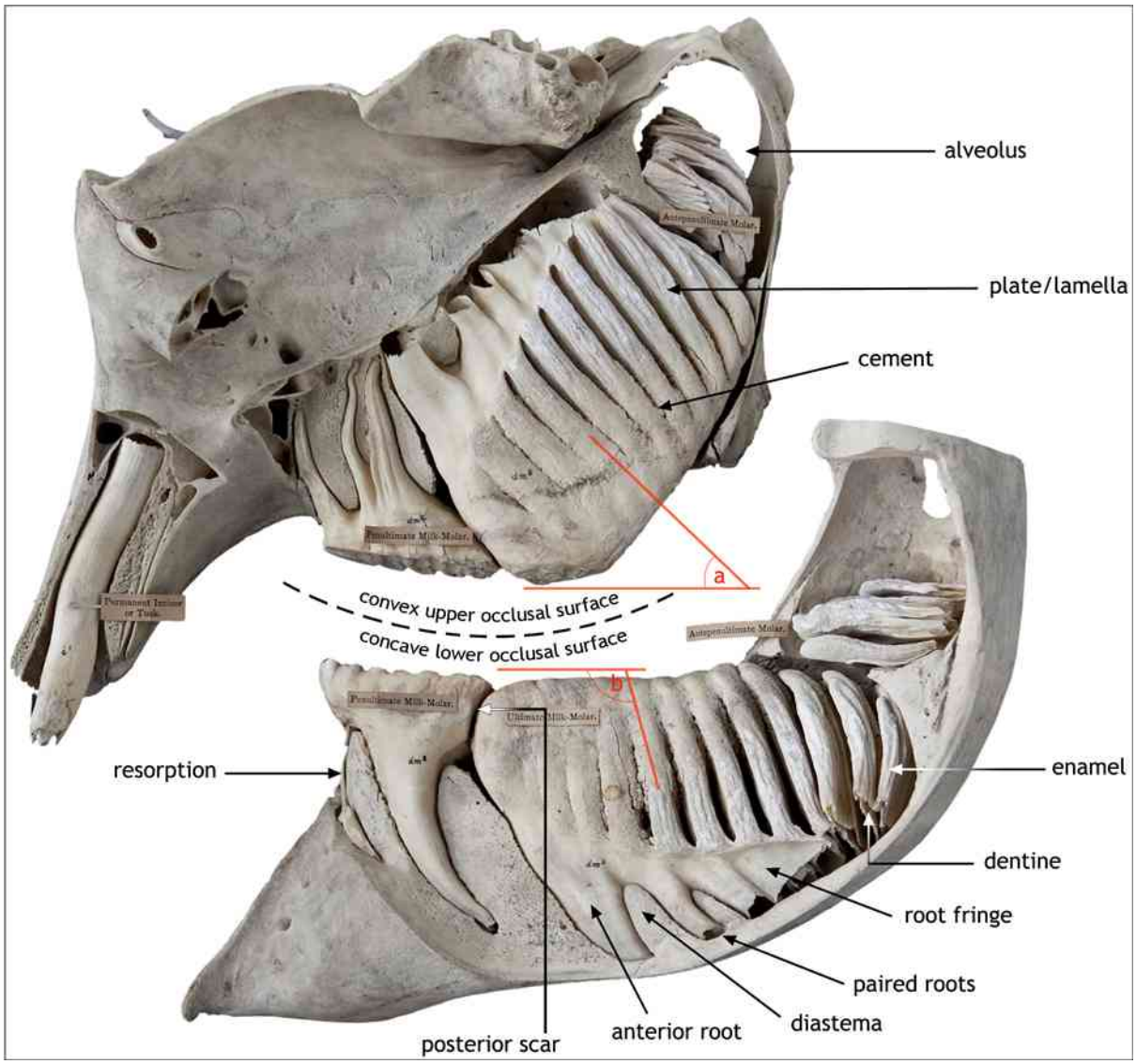

Figure 2.1. Characteristics of elephant molar morphology and tooth progression. Longitudinal section of a juvenile *E. maximus* skull (approximately 3-4 years old based on molar wear; Laws 1966, Roth & Shoshani 1984). dP3 and dP4 are in wear, and M1 is beginning to form in the posterior alveolus. The lingual edge of the maxillary and mandibular bone is cut away to expose the dentition, and clearly shows the mesiodistal axis of wear and of plate and root formation. Anterior plates are more heavily worn, with the front-most plates and roots of dP3 also undergoing resorption. More posteriorly, cement has yet to form around the plates. The most posterior plates are not fully-formed, and are loose in the alveolus. Their structure as an enamel 'pocket' can be seen; in life, they would be filled with dentine. The pressure scar on the posterior end of the lower dP3, caused by the forward progression of dP4, is also visible. Differences in upper and lower morphology (mentioned in the text) are evident, in particular the angle between the vertical plate-axis and the occlusal plane. Upper molar plates form an acute angle (**a**), while lower molar plates meet the occlusal plane at an angle much closer to 90° (**b**). Photocredit: NHM photo unit. Copyright NHM.

Molar identification

The homology of elephant teeth with those of other mammals is controversial (Maschenko & Kalmykov 2009). However, only the homology of teeth within the Elephantidae affects analyses and interpretation of results in this study, and I follow the widely-used nomenclature of Aguirre (1969) and Maglio (1973). Teeth are thus referred, from developmentally youngest to oldest, to: dP2, dP3, dP4 (the deciduous pre-molars) and M1, M2, M3 (the permanent molars).

Identifying an isolated elephant tooth to its place within the dental series is challenging as teeth are largely similar in morphology, and often delineated from one another on the basis of size (Roth 1982). This is particularly problematic for a study of dwarf elephants, where we cannot assume *a priori* that a sample contains a single species of a particular size. Fortunately, dP2 and M3 (and to a lesser extent dP3) teeth have distinctive morphologies, providing fixed size-points at either end of a molar series: dP2 resembles post-canine teeth in other mammals, with 1-2 roots and 3-4 plates (Maschenko & Kalmykov 2009), while M3 is highly curved bucco-lingually, and tapers posteriorly (in both width and crown height; Figure 2.3, Maglio 1973). Pre-M3 teeth can be identified by their flat posterior ends, and are often marked by a 'posterior scar' caused by the pressure of the tooth behind it (Figure 2.3). The anterior end of an elephant molar can be identified by the wear pattern (the front end of the tooth is the most worn) or, in unworn teeth, by the presence of the anterior root (a large, unpaired root positioned towards the convex side of the tooth, and often with a gap or 'diastema' between it and the paired roots) (Figure 2.1).

Upper and lower molars differ in their morphology, and must be analysed separately (within a species, upper molars tend to be wider and higher crowned). Uppers can be identified by their approximately straight, parallel plates which meet the occlusal plane at an acute angle (Figure 2.1). The occlusal surface is also convex bucco-lingually and mesio-distally (Figure 2.1). In comparison, lower molars have plates which converge towards the mesio-distal apex of the tooth, and can be sinusoidal in shape (e.g. Figure 2.3). The occlusal plane is approximately perpendicular to the average plate axis in lower molars, and the occlusal surface is concave (Figure 2.1).

Left and right molars of the same individual have been shown to not differ significantly from each other (Roth 1982, Haynes 1991, Davies 2001, Chang 2010). They are thus combined in this study to maximise sample size; however tooth side was identified for future reference. Upper molars tend to curve in the direction of the jaw and are convex on the buccal side, while lower molars curve in the opposite direction and are convex on the lingual side. Additionally, upper and lower teeth wear assymetrically in the bucco-lingual plane. Uppers wear more on the lingual side, while lowers wear more on buccal side. By holding an isolated tooth so that its occlusal surface faces up, and its anterior end points away from the viewer, both upper and lower teeth can be identified as left or right as follows:

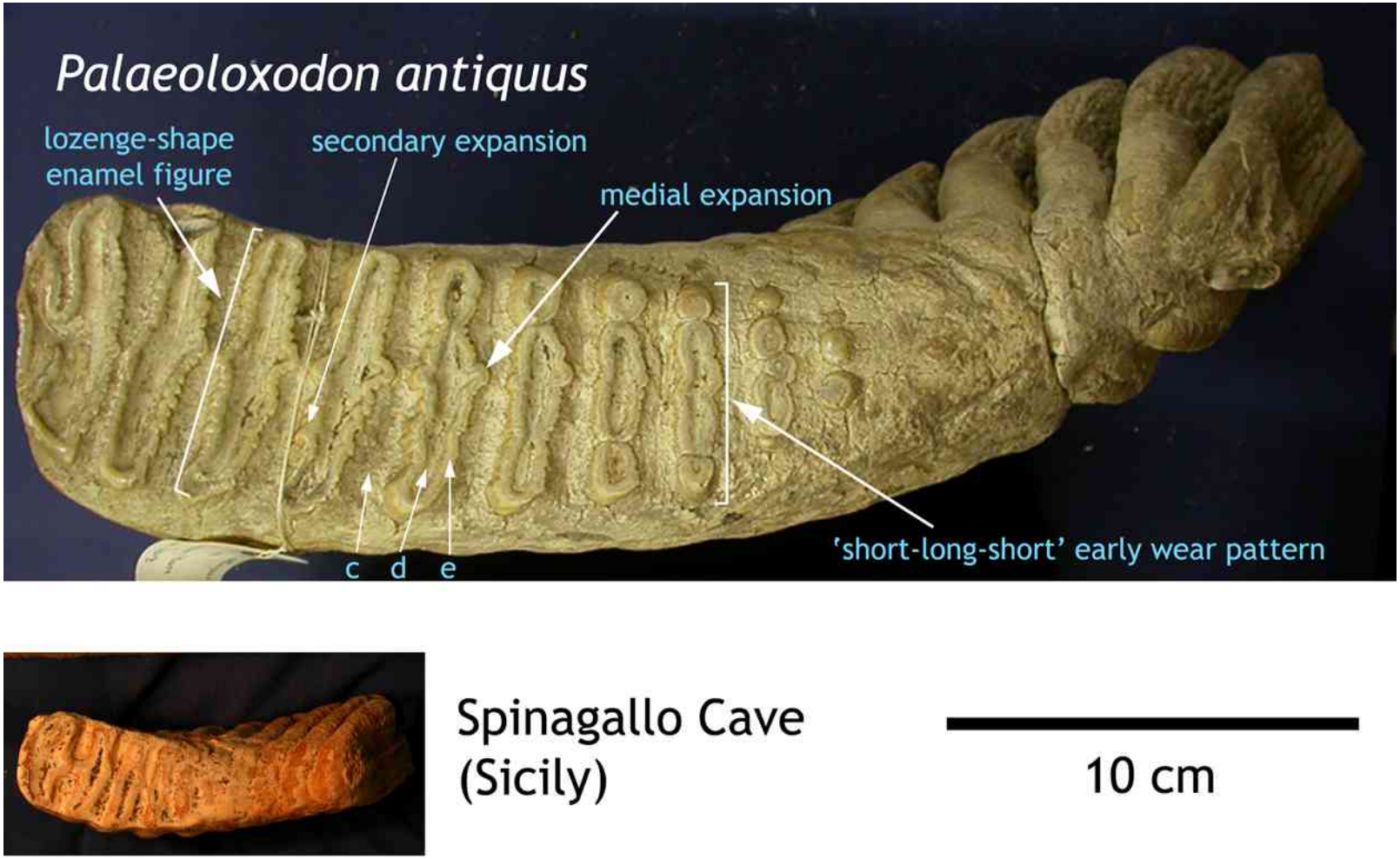

Figure 2.2. Features of the occlusal surface and characteristics of *P. antiquus*. Lower M3 of *P. antiquus* (above) and *P. falconeri* from Spinagallo Cave (below), to the same scale. As plates wear down, they are exposed in cross-section through the occlusal plane, forming a series of enamel (**e**) loops or 'figures' along the occlusal surface. Each loop has a dentine-filled (**d**) centre, and the plates are encased in cement (**c**). The enamel figure is taxonomically informative in both early (toward the right of the picture) and middle-late (towards the left of the picture) wear. A relatively narrow tooth, with lozenge-shaped enamel figure and medial expansions in middle wear, is diagnostic for *Palaeoloxodon,* as is the early wear pattern of a long central enamel loop, flanked by two shorter loops (see Chapter 4). The features can also be seen in the Spinagallo Cave specimen, although enamel is less folded.

1. on the basis of the bucco-lingual curve of the tooth: if the concave side of the tooth is on the left, then the tooth is from the left side; if the concave side is on the right, then the tooth is from the right side.
2. on the basis of wear viewed in the bucco-lingual plane: left molars have their lowest edge on the left side, while right molars have their lowest edge on the right side

Molar variables and indices

Molar variables and measurement protocols, following Maglio (1973), are described in Tables 2.3 and 2.4, and illustrated in Figure 2.3. In addition to these raw measurements, two widely-used indices are calculated: Hypsodonty Index (HI) and Lamellar frequency (LF). Measurements were taken using either digital calipers (accurate to 0.1 mm; up to 150 mm) or sliding calipers with adjustable 'jaws' (accurate to 1 mm; up to 300 cm). The most accurate tool possible was usually chosen for each measure. For some measurements <150mm, this might mean using the larger, less precise calipers if longer caliper 'jaws' were needed to accurately capture the measurement. All variables were tested for repeatability (Appendix 2), and had acceptable repeat measurement error (less than 5%; White 1991).

Hypsodonty Index is a measure of relative crown height, and is calculated by:

$$HI = CH/W*100 \quad [2.1]$$

where CH is the unworn crown height, and W is the molar width (Table 2.3)

If calculated from almost complete but worn plates, hypsodonty index would be underestimated. I refer to this as the Minimum Hypsodonty Index:

$$MinHI = MCH/W*100 \quad [2.2]$$

where MCH is the minimum crown height, and W is the molar width (Table 2.3)

Hypsodonty Index provides a size-independent index of tooth shape, and is thus useful for comparing gross tooth morphology between dwarf taxa of different sizes, and between full-sized and dwarf taxa.

Lamellar frequency is an index of how closely packed the plates are within a tooth. It is often used to identify 'advanced', or more derived, evolutionary forms within an evolving lineage, as there has been a parallel evolution of increasingly close-packed plates over time in both *Elephas* and *Mammuthus* (linked with grazing adaptation: Maglio 1972, 1973; Lister & Joysey 1992). As an index for evolutionary change, it is unable to differentiate between a change in size, or a change in plate number, and can thus can obscure trends if used in isolation. It is best considered in relation to another proxy of molar size to tease apart these factors (Lister & Joysey 1992; Chapter 6)

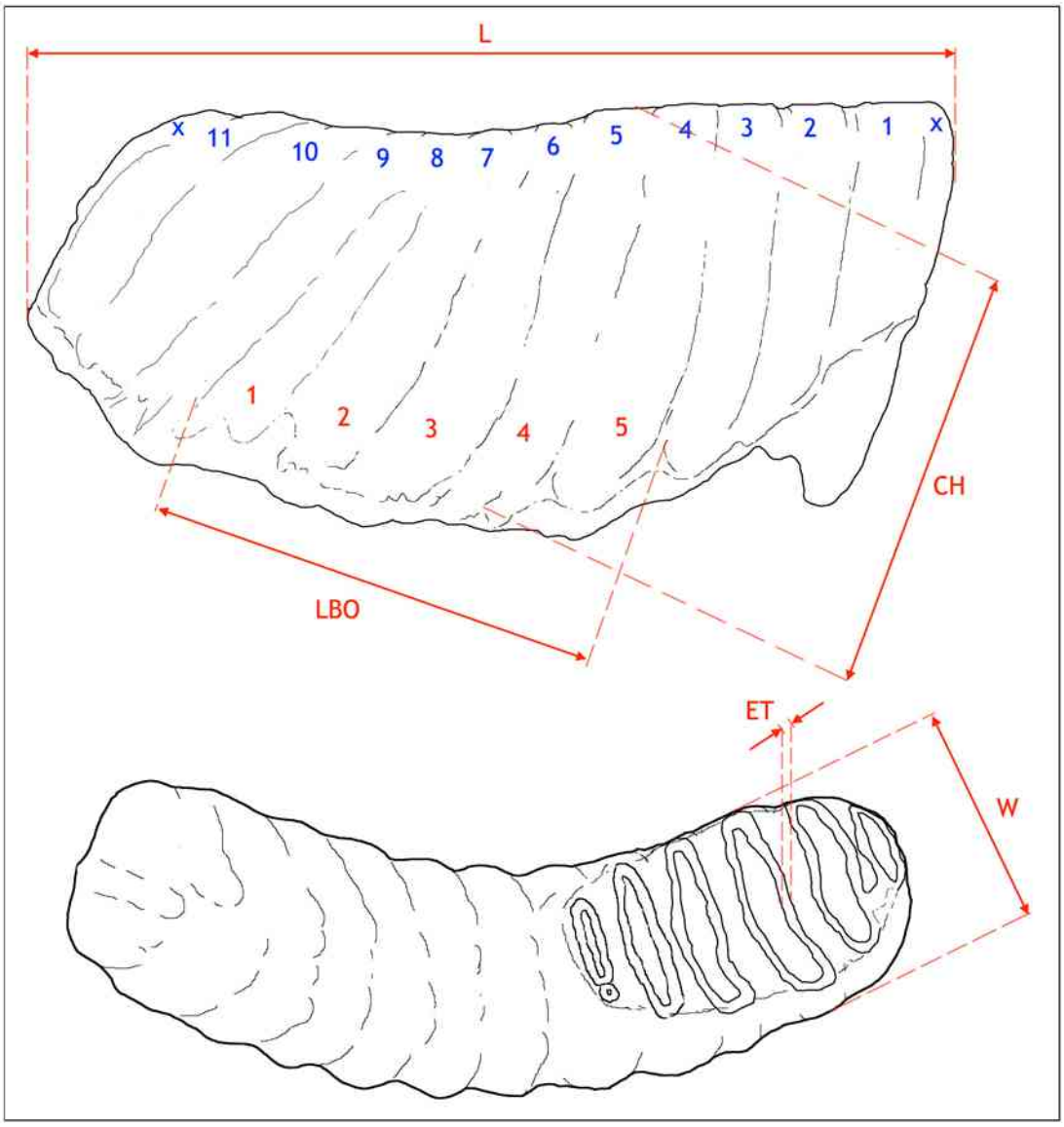

Figure 2.3. Molar measurements included in this study. Illustrated using a lower left M3 of *P. cypriotes*. See Table 2.3 & 2.4 for measurement protocols and abbreviations. Blue numbers indicate the total tooth plate count, while red numbers indicate the number of plates in the LBO region, to be used in the calculation of lamellar frequency. Note that LBO and L are taken roughly perpendicular to the average direction of the plates within their sample region, while CH is taken parallel to the vertical axis of the plate on which it is measured. LBO includes one cement interval per plate, hence its extension beyond plate 5 to the edge of the adjacent plate. Measurements for upper molars are not shown, but are equivalent; however care must be taken to ensure caliper prongs are perpendicular to the average plate angle and **not** to the occlusal surface when taking length measures

Variable	Abbrev.	Description/Protocol	Notes
Plate Count	PC	A meristic count of the number of plates in the tooth, from anterior to posterior of tooth; small anterior and posterior plates, with no root and which are fused with adjoining plates are identified as 'talons' (= 'x'), and are not included in PC (e.g. tooth with 13 plates and anterior and posterior talon = x13x)	1. Only use PC in statistical analyses if a good estimate of true plate count (true front of tooth, with anterior root present; true back of tooth present). 2. If anterior plates are lost to wear, precede PC with '∞' (e.g ∞12x) 3. Indicate missing anterior or posterior plates, owing to breakage or because they have yet to form/fuse to main body of tooth, with '-' (e.g. missing anterior plates: -12x; missing posterior plates x12-; anterior & posterior missing: -12-) 4. Note number of plates in wear, and wear stage of tooth as 'early', 'middle' or 'late' (see text for explanation) for future reference
Maximum Width	Width, W	Maximum width of tooth, across the widest plate (in mm); calipers in-line with bucco-lingual axis of plate, ensure caliper prongs reach maximum width of plate below the crown	1. Estimate how much cement included, and subtract from measurement. 2. Indicate if good estimate of 'true' maximum width. 3. Note plate number measurement taken on, from back and front of tooth.
Maximum Length	Length, L	Maximum length of tooth in mm, taken perpendicular to average antero-posterior angle of plates	Only take on teeth estimated to be over 95% complete (anterior root and talon present; tooth in 'early wear'; true posterior of tooth present).
Unworn Crown Height	CH	Maximum height of tooth in mm, from the crown to the base (where the root begins) of an unworn plate; calipers parallel to vertical axis of plate. Take on side of tooth which wears down less (lingual for lowers, buccal for uppers)	1. Note plate number measurement taken on, from back and front of tooth. 2. Take only if confident plate height is a good estimate of true crown height (i.e. more anterior plates would not be taller in unworn state; posterior plates are shorter; in region of maximum crown height *sensu* Sher & Garutt 1987).
Minimum Crown Height	MinCH, MCH	As CH, but taken from worn plates or unworn plates which are likely to be shorter than maximum crown height	1. Note plate number measurement is taken on, from back and front of tooth. 2. Only take on worn plates that are likely to be good estimates of 'true' crown height
Average Enamel Thickness	ET	Thickness of enamel ridge in mm; caliper prongs parallel to vertical axis of plate (**not** perpendicular to occlusal surface); avoid medial expansions and tightly folded regions where possible	Repeat 10 times, at different points on occlusal surface, and use average (mean) value.

Table 2.3. Upper and lower molar variables and measurement protocols employed in this study. Protocols are applicable to both upper and lower molars, as long as directions pertaining to plate-axes are followed. See also Figure 2.2. Abbrev. is Abbreviation

Variable	Abbrev.	Description/Protocol	Notes
Number of plates on:			
base of crown, convex (‘outer’) side	NBO	Meristic count of plates in a well preserved, central region of the tooth	1. minimum of 3 plates, preferably >5 2. LBO & LBI on upper and lower molars 3. LTO & LTI on upper molars only
base of crown, concave (‘inner’) side	NBI		
top of crown, convex (‘outer’) side	NTO		
top of crown, concave (‘inner’) side	NTI		
Length of region of N plates for:			
base of crown, convex (‘outer’) side	LBO	length in mm across N plates, including 1 cement interval per plate; taken perpendicular to average A-P angle of plates	1. LBO & LBI on upper and lower molars 2. LTO & LTI on upper molars only
base of crown, concave (‘inner’) side	LBI		
top of crown, convex (‘outer’) side	LTO		
top of crown, concave (‘inner’) side	LTI		

Table 2.4. Molar measurements and protocols for calculating lamellar frequency. See text for calculation of lamellar frequency (LF). The terms ‘outer’ and ‘inner’ are used here to refer to the outer and inner edges of a curve, and are not equivalent to buccal and lingual, see text for explanation. See also Figure 2.2. Abbrev. is abbreviation.

Lamellar frequency could be calculated from the total number of plates in a tooth divided by the tooth length, but to maximise sample sizes it is instead calculated from a smaller region of the tooth (thus enabling the inclusion of fragmentary specimens). However, Lamellar Frequency should only be taken in a central portion of the tooth, and on a minimum of three plates (preferably more than five) (Maglio 1973). Formally defined as the number of plates in 100mm, Lamellar frequency is calculated as follows:

$$LF_{(upper\ molar)} = [(NBO/LBO)+(NBI/LBI)+(NTO/LTO)+(NTI/LTI)]/4 \quad [2.3]$$

$$LF_{(lower\ molar)} = [(NBO/LBO)+(NBI/LBI)]/2 \quad [2.4]$$

see Table 2.4 for abbreviations and protocols

Lamellar frequency is thus an average value of 'plate packing', as calculated from both the buccal and lingual sides of the tooth, to correct for the effect of tooth curvature (see above). The typical curvature of buccal and lingual sides of the tooth is dependent on whether it is upper or lower, thus for ease of comprehension I refer to the 'convex' or the 'concave' side of the tooth to indicate which side of the molar-curvature I am measuring. However, as both these terms start with the same letter, I abbreviate convex to 'O' (the 'outer' edge of the curve), and concave to 'I' (the 'inner edge of the curve) in tables and figures.

LF is calculated only from base-of-crown measures in lower molars to ensure comparability across different wear-stages (lower molar plates converge towards the crown apex, and thus LF would be variable through crown height; Lister & Stuart, in press). An average of four measures is still used for upper molars (where plates are parallel and thus not affected by wear in the same way), as this method appears to minimise measurement error, and increase repeatability. Although LF is size-corrected, it has been shown to vary intraspecifically with molar size (larger teeth tend to have lower LF values) (Lister & Joysey 1992), and may not be size-independent in a biological sense. Allometric trends in this variable are explored further in Chapter 6.

2.2.2. Postcrania

Data were collected from the four major long-bones: the humerus, ulna, femur and tibia. I aim to characterize broad patterns of inter- and intraspecific limb bone scaling in dwarf and full-sized elephants, including across post-natal ontogeny. These four bones were chosen as they are (i) widely represented in collections, (ii) easy to identify, even in neonates, (iii) sufficiently ossified in juveniles to produce a series of variables that could be applied across the full age-range, (iv) widely incorporated into biomechanical scaling studies, facilitating comparisons with the literature, and (v) implicated in dwarf elephant adaptation (Sondaar 1977). Other post-cranial bones were more prone to breakages (radius and fibula); or were difficult to identify with confidence in dwarf elephants (metatarsals and metacarpals); or were under-represented in collections, preventing interspecific comparisons (scapula and pelvis).

Measurements had to be common to both juvenile and adult specimens. Chapter 5 outlines the protocol for assessing epiphyseal fusion, and how I identified adult bones in this study. As epiphyses are unfused in juvenile specimens, epiphyseal measurements, or measurements that relied on the presence of the epiphyses, could not be included. Instead, I focus on the morphology of the diaphysis, following Roth (1982). Bilateral symmetry was assumed, and left and right bones were pooled to maximise sample sizes. If an associated skeleton was measured, bones from one side only were included to avoid duplication and sample bias. Measurement protocols with accompanying notes are outlined in detail in Tables 2.5-2.8 and Figures 2.4-2.7. All variables were tested for repeatability (Appendix 2), and had acceptable repeat measurement error (less than 5%; White 1991).

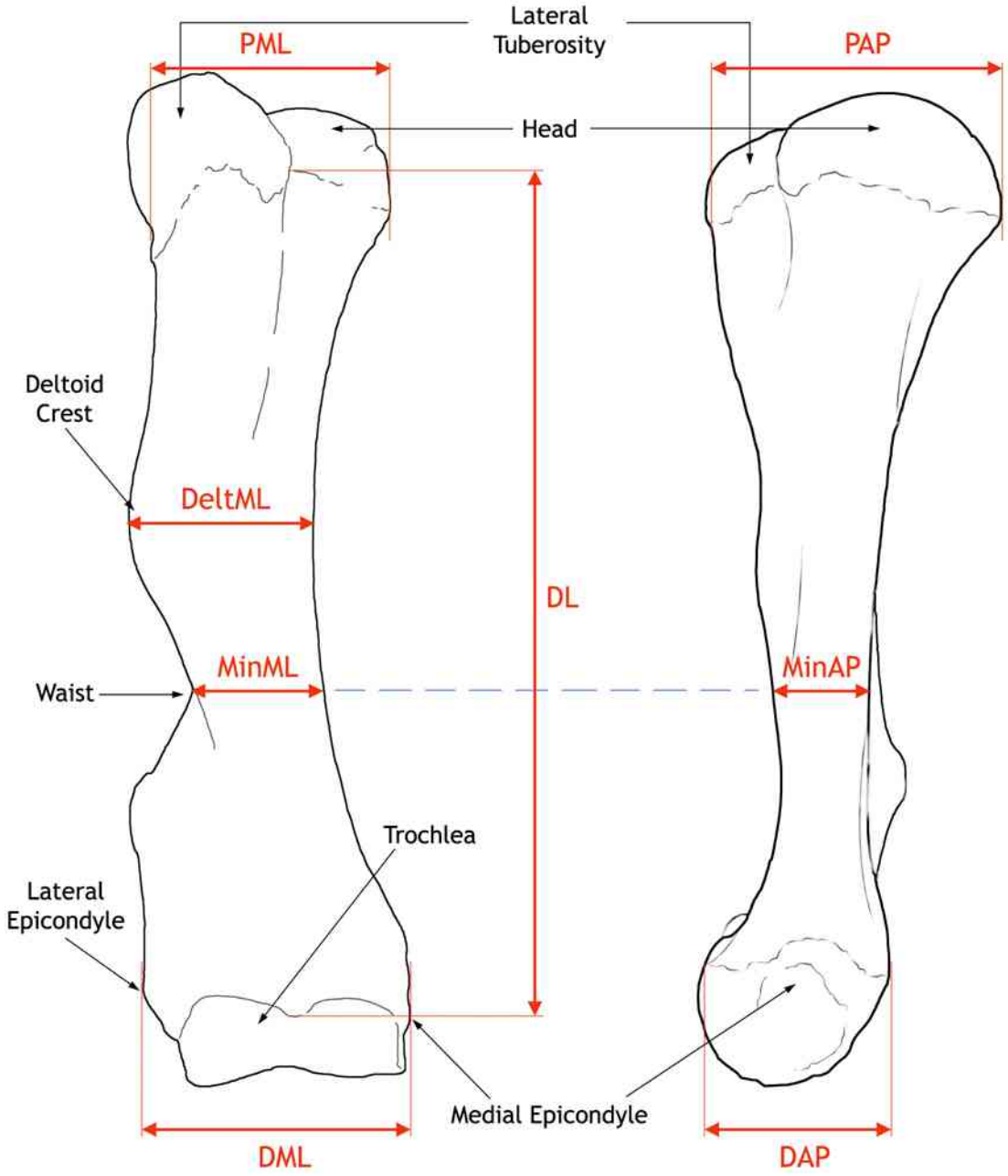

Figure 2.4. Measurements taken on the humerus. Illustrated on anterior (left) and medial (right) views of a right-side *L. africana* specimen. See Table 2.5 for measurement protocols, notes and abbreviations. Blue dashed line indicates that MinAP should be taken at the same point along the shaft as MinML (which is found by locating the narrowest point of the humerus 'waist'). There is some degree of torsion through the humeral shaft, hence 'ML' and 'AP' direction are taken perpendicular to the ML axis at that point in the shaft, to ensure repeatability and consistency when measuring fragmentary specimens.

Variable	Abbrev.	Description/Protocol	Notes
Diaphysis length	DL	Diaphysis length (in mm), between the proximal and distal epiphyseal lines; taken parallel to the long-axis of the humerus, on the anterior surface, along the mid-line of the diaphysis	
Proximal medio-lateral diaphyseal width	PML	Maximum ML width (in mm) across the proximal epiphyseal line; taken perpendicular to ML axis of proximal epiphysis	If epiphyseal line is obliterated, or obscured by rugose bone on lateral tuberosity, widths will be exaggerated
Proximal antero-posterior diaphyseal width	PAP	Maxiumum AP width (in mm) across the proximal epiphyseal line; taken from the medial side, perpendicular to PML, with caliper prong-tips along the mid-line of the shaft. Includes the most anterior point of the proximal diaphysis leading to the lateral tuberosity, and the most posterior point of the proximal diaphysis below the head.	If epiphyseal line is obliterated, or obscured by rugose bone on lateral tuberosity, widths will be exaggerated
Max medio-lateral width across the deltoid crest	DeltML	Maximum diaphyseal width (in mm) across the deltoid crest (Figure 2.4); taken perpendicular to the ML axis of the diaphysis at this point along the shaft	Find maximum width by gently running calipers along edge of shaft in the deltoid crest region.
Minimum medio-lateral width	MinML	Minimum ML width (in mm); taken at the humeral 'waist' (Figure 2.4), perpendicular to the long-axis of the diaphysis	Find waist by gently running caliper prongs along diaphysis between the deltoid crest and the lateral epicondyle; the 'nadir' of the curve is the waist.
Minimum antero-posterior width at the humeral 'waist'	MinAP	AP width (in mm) taken perpendicular to MinML, at the same point along the shaft	1. This may not be the minimum AP width of the shaft; 'MinAP' is used for consistency with MinML. 2. measurment must be taken at same point as MinML, rather than an independent minimum AP value found by running calipers along shaft
Distal medio-lateral diaphyseal width	DML	Maximum ML width (in mm) across the lateral and medial epicondyles (Figure 2.x), at the epiphyseal line; taken perpendicular to the ML-axis of the distal epiphysis	The lateral epicondyle has a separate fusion surface to the distal epiphysis, and both epicondyles become increasingly rugose with age; juvenile distal width are thus not exact homologues of adult widths, and may overestimate any increase in robustness with age
Distal antero-posterior diaphyseal width	DAP	Maximum AP width (in mm) across the medial epicondyle (Figure 2.x), at the epiphyseal line; taken perpendicular to the long-axis of the humerus	

Table 2.5. Humerus variables and measurement protocols employed in this study. ML is medio-lateral, AP is antero-posterior. See Figure 2.4 for anatomical details and further information. Abbrev. is abbreviation.

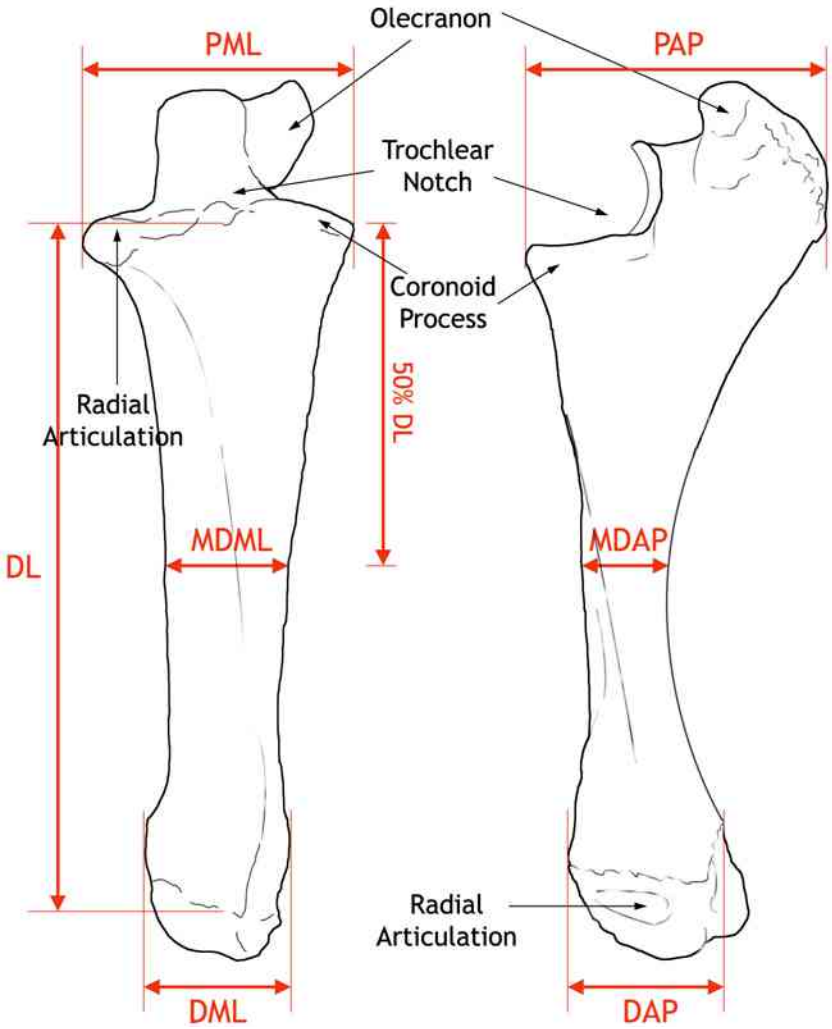

Figure 2.5. Measurements taken on the ulna. Illustrated on anterior (left) and medial (right) views of a right-side *L. africana* specimen. See Table 2.6 for measurement protocols, notes and abbreviations. The radius head articulates on the lateral side of the trochlear notch, to form part of the articular surface of the hinge-like joint with the distal humerus. The radius shaft then twists around the anterior surface of the ulna shaft (its path can be traced by the visible diagonal ridge) to articulate on the medial edge of the distal epiphysis. Some elephants (more common in dwarfs) show fusion between the radius and the ulna, and in extant, or mounted skeletons, these bones are also sometimes held together (either by flesh, or by screws or wires). In these situations a number of measurements are not possible (see Table 2.6).

Variable	Abbrev.	Description/Protocol	Notes
Diaphysis length	DL	Diaphysis length (in mm), between the proximal end of the diaphysis, just below the trochlear notch (Figure 2.5) and the distal epiphyseal line; taken parallel to the long-axis of the ulna, on the anterior surface, along the mid-line of the diaphysis	
Proximal medio-lateral diaphyseal width	PML	Maximum ML width (in mm) across the trochlear notch at the level of the coronoid process (Figure 2.5); taken perpendicular to ML axis of proximal epiphysis	Not suitable for bones fused with radius
Proximal antero-posterior diaphyseal width	PAP	Maximum AP width (in mm) from the most anterior point on the coranoid process to the most posterior point of the diaphysis below the olecranon process; taken on the medial side, perpendicular to AP-axis of ulna	
Maximum midshaft medio-lateral width	MDML	Maximum ML width (in mm) across the diaphysis at 50% DL, perpendicular to the long-axis of the ulna	
Maximum midshaft antero-posterior width	MDAP	Maximum AP width (in mm) across the diaphysis at 50% DL, taken perpendicular to MDML	Not suitable for bones fused with radius
Distal medio-lateral diaphyseal width	DML	Maximum ML width (in mm) of the distal diaphysis, taken across the distal epiphyseal line	Not suitable for bones fused with radius
Distal antero-posterior diaphyseal width	DAP	Maximum AP width (in mm) of the distal diaphysis, taken across the distal epiphyseal line; taken perpendicular to the A-P axis of the distal ulna	

Table 2.6. Ulna variables and measurement protocols employed in this study. ML is medio-lateral, AP is antero-posterior. See Figure 2.5 for anatomical details and further information. Abbrev. is abbreviation.

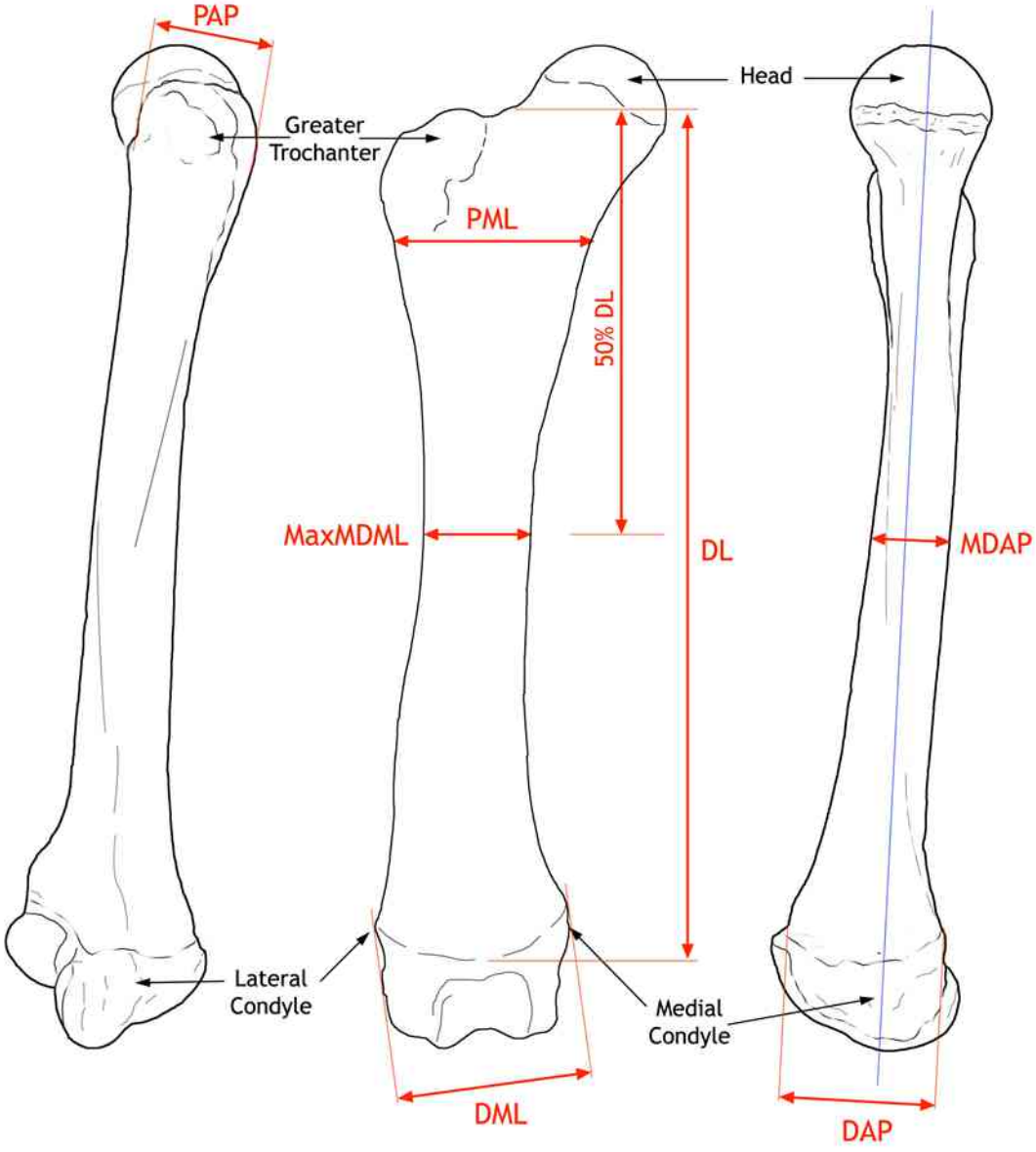

Figure 2.6. Measurements taken on the femur. Illustrated on lateral (left) anterior (centre) and medial (right) views of a right-side *L. africana* specimen. See Table 2.7 for measurement protocols, notes and abbreviations. There is some torsion and antero-posterior bending through the femoral shaft, hence 'ML' and 'AP' measurements are taken perpendicular to the ML axis at that point in the shaft, and to the long-axis (e.g. blue line) of the shaft to ensure repeatability and consistency when measuring fragmentary specimens.

Variable	Abbrev.	Description/Protocol	Notes
Diaphysis length	DL	Diaphysis length (in mm), between the proximal and distal epiphyseal lines; taken parallel to the long-axis of the femur, along the mid-line of the diaphysis (proximal epiphysis measured from approximate point where GT fusion surface meets neck, which is near the shaft mid-line)	
Proximal medio-lateral diaphyseal width	PML	Maximum ML width (in mm) across the diaphysis, taken at the level of the distal-most point of the epiphyseal line of the greater trochanter	Older individuals may have a rugose GT, while GT is absent in unfused juveniles; width differences may be accentuated, although this is minimized by taking ML width just below the GT
Proximal antero-posterior diaphyseal width	PAP	Maximum AP width (in mm), taken at the same level as MDML; taken on lateral side (just below GT), parallel to the AP-axis of the proximal femur	
Maximum midshaft medio-lateral width	MDML	Maximum ML width (in mm) across the diaphysis at 50% DL, perpendicular to the long-axis of the femur	
Maximum midshaft antero-posterior width	MDAP	Maximum AP width (in mm) across the diaphysis at 50% DL, taken perpendicular to MDML	
Distal medio-lateral diaphyseal width	DML	Maximum ML width (in mm) off the distal diaphysis, taken across the epiphyseal line	In older individuals, rugosity of lateral and medial condyles may obstruct calipers and exaggerate width
Distal antero-posterior diaphyseal width	DAP	Maximum AP width (in mm) off the distal diaphysis, taken across the epiphyseal line and perpendicular to DML	

Table 2.7. Femur variables and measurement protocols employed in this study. ML is medio-lateral, AP is antero-posterior. See Figure 2.6 for anatomical details and further information. GT is greater trochanter. Abbrev. is abbreviation.

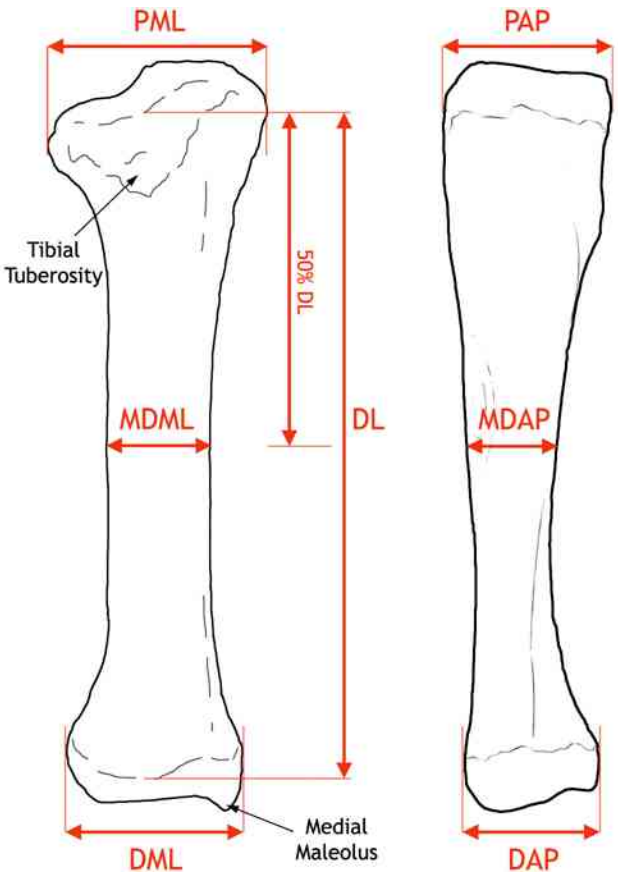

Figure 2.7. Measurements taken on the tibia. Illustrated on anterior (left) and medial (right) views of a right-side *L. africana* specimen. See Table 2.8 for measurement protocols, notes and abbreviations.

Variable	Abbrev.	Description/Protocol	Notes
Diaphysis length	DL	Diaphysis length (in mm), between the proximal and distal epiphyseal lines; taken parallel to the long-axis of the tibia, along the mid-line of the diaphysis	Tibial tuberosity (TT; Figure 2.7) may obscure the anterior surface of the proximal epiphyseal line in older individuals; in these cases the proximal most point of the diaphysis is estimated from the top of the rugose region of the TT
Proximal medio-lateral diaphyseal width	PML	Maximum ML width (in mm) across the diaphysis, taken across the epiphyseal lines, perpendicular to the ML-axis of the proximal tibia	Not suitable for bones fused with fibula
Proximal antero-posterior diaphyseal width	PAP	Maximum AP width (in mm); taken on medial side, across the epiphyseal line and perpendicular to MDML	
Maximum midshaft medio-lateral width	MDML	Maximum ML width (in mm) across the diaphysis at 50% DL, perpendicular to the long-axis of the tibia	Only suitable for bones fused with fibula if caliper prongs can be easily inserted between tibia and fibula on lateral edge of tibia
Maximum midshaft antero-posterior width	MDAP	Maximum AP width (in mm) across the diaphysis at 50% DL, taken perpendicular to MDML	
Distal medio-lateral diaphyseal width	DML	Maximum ML width (in mm) off the distal diaphysis, taken across the epiphyseal line	Not suitable for bones fused with fibula
Distal antero-posterior diaphyseal width	DAP	Maximum AP width (in mm) off the distal diaphysis, taken across the epiphyseal line and perpendicular to DML	

Table 2.8. Tibia variables and measurement protocols employed in this study. ML incomiis medio-lateral, AP is antero-posterior. TT is tibial tuberosity. See Figure 2.7 for anatomical details and further information. Abbrev. is abbreviation.

Chapter 3: Palaeogeography and Geochronology

The use of process-based reasoning (see 4.1.2 for discussion) in dwarf elephant systematics necessitates a careful audit of the provenance of the dwarf elephant material under study. The geographical and geological provenance of each specimen establishes a primary hypothesis of conspecifity: are specimens from the same stratigraphical level/geological age, on the same island a single species? Establishing a fossil species in space and time is also vital for the investigation of evolutionary trends. Understanding the limitations of this knowledge is, however, equally important. In this chapter I summarize and evaluate the published data for Mediterranean dwarf elephant geographic and temporal distribution. I consider the impact of geo-morphological change and sea-level changes on dwarf elephant palaeogeography, and take a three-step approach to assessing temporal distribution. First, I assess the impact of site-sampling biases on the evolutionary hypotheses that can be tested, and use site description summaries (Appendix 1) to establish known stratigraphical provenance and faunal association of the dwarf elephant material included in this study. Second, I evaluate the reliability of published dates for dwarf elephants. Third, I consider island-wide correlations between the published dates, taxa and faunal association (biostratigraphy) established from steps one and two, along with additional published information, to identify (i) co-eval populations of dwarf elephants and (ii) the relative ages of non-coeval populations. This information is used to formulate further hypotheses of conspecifity for testing in Chapter 4.

3.1. Geographical distribution of Mediterranean dwarf elephants

Dwarf elephant fossils are known from twelve Mediterranean islands: Sardinia, Sicily, Malta, Crete, Cyprus, Tilos, Rhodes, Delos, Serifos, Milos, Kythnos and Naxos. This study focuses on the material collected on five of these islands (Figure 3.1), balancing the desire for an exhaustive survey of all Mediterranean dwarf elephants with the practicalities of time (and financial) constraints and access to material. These islands (Sicily, Malta, Crete, Cyprus and Tilos) were selected because they encompass the Eastern and Western Mediterranean basins, have the largest and most historically important dwarf elephant collections and cover the full stratigraphic and body size range of Mediterranean elephants.

The fossil localities for the dwarf elephant localities included in this study (Figure 3.1; Appendix 1) are also not exhaustive: there is discrepancy between the number of sites sampled and the total number of sites for each island, and this impacts on the hypotheses that can be tested (Table 3.1). To the best of my knowledge, I have included every dwarf elephant locality on Malta for which there is relatively complete material (five sites; Appendix A1.1) and on Tilos (one site; Appendix A1.5). For Sicily, Cyprus and Crete, where there are a large number of localities that have only yielded one or two fragmentary specimens, this was impossible owing to access restrictions and feasibility issues.

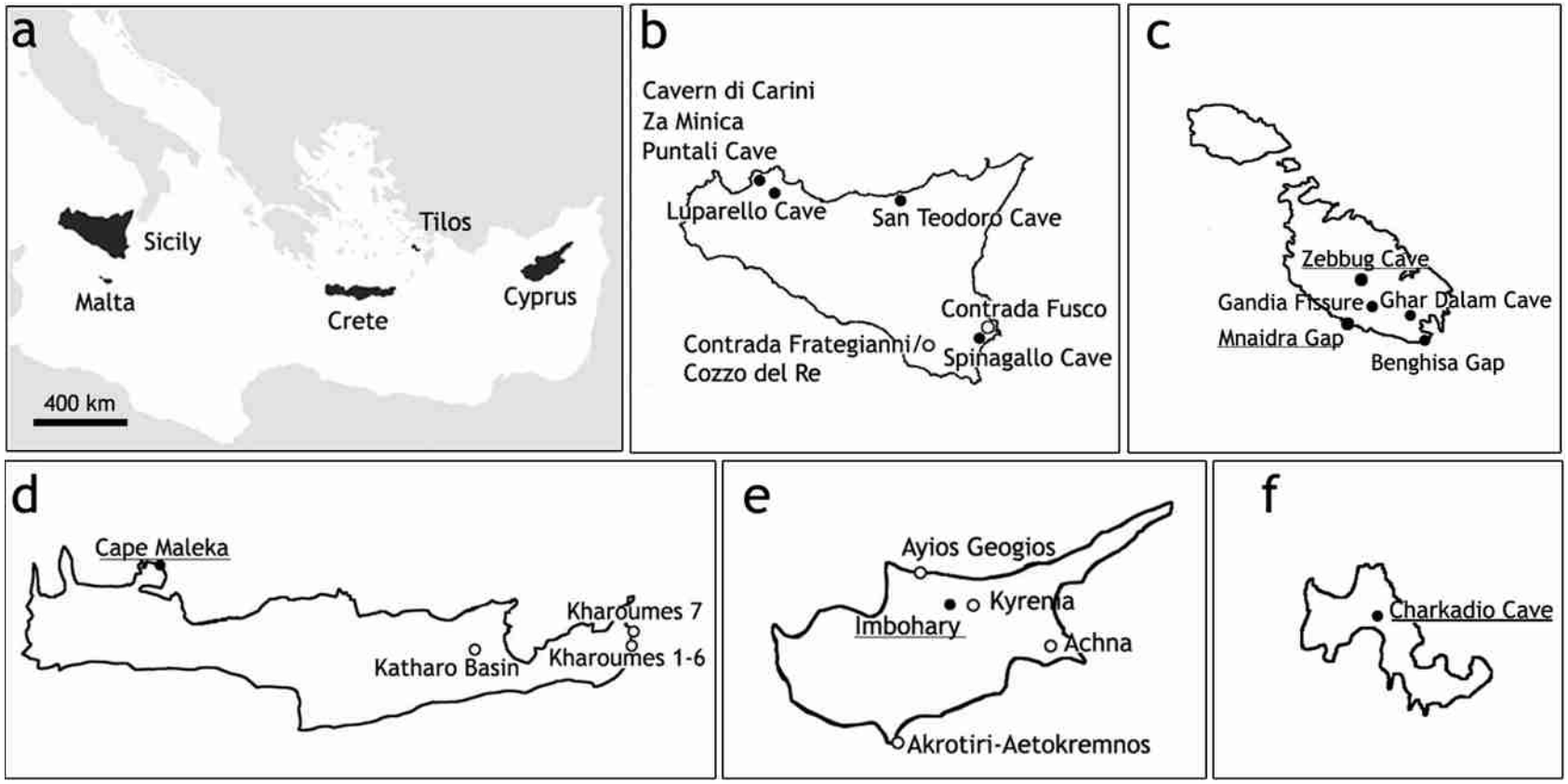

Figure 3.1. Mediterranean dwarf elephant fossil localities. a. map of Central and Eastern Mediterranean. Islands included in this study are shaded black. **b.** Sicily, **c.** Malta, **d.** Crete, **e.** Cyprus, **f.** Tilos. Filled circles are localities of material included in this study; open circles are fossil localities referred to in the text (e.g. for stratigraphical correlation purposes), but not included in this study; type localities are underlined. Islands in b-f are not drawn to the same scale.

On Sicily, all sites of historical importance which had large dwarf elephant collections are included (these characteristics generally covary; five sites, Appendix A1.2). Notable omissions are Contrada Fusco and material from Contrada Frategianni and Cozzo del Re (potentially the oldest dwarf elephant fossils on Sicily, (Bonfiglio & Insacco 1992)), as well as the numerous North-West coast sites. I was unable to arrange access to the material from these sites.

The only *M. creticus* locality on Crete, Cape Maleka, is included (Appendix A1.3). However, material deriving from multiple localities and attributed to *P. creutzburgi* was unavailable for study (it was placed in storage while a new museum in Rethymnon was built). This restricts my analysis of Cretan dwarf elephants to *M. creticus*. Katharo Basin and the Kharoumes localities (Figure 3.1) have played key roles in the Pleistocene geochronology of Crete.

Again, on Cyprus, I was only able to access material from a single *P. cypriotes* locality, the type locality Imbohary (Appendix A1.4). However, this site has the largest collection of complete or nearly complete elephant molars. I was unable to gain access to fossils from the other major *P. cypriotes* site, Akrotiri Aetokremnos (Figure 3.1), and thus cannot verify the taxonomic affinity of this material. This is particularly unfortunate as Akrotiri Aetokrmenos has been extensively dated (discussed below), while Imbohary has not. Elephant material is rare at all Cypriot Pleistocene localities (which are dominated by the pygmy hippopotamus *Phanourios minor*), and the remainder of the *P. cypriotes* material is dispersed over numerous localities, and housed in several private collections (Reese 1995). It was not feasible to arrange visits to each of these collections, especially as the material is generally fragmentary (e.g. isolated plates). For similar reasons, I was unable to include the large-sized Cypriot elephant from sites such as Achna. As such, I cannot fully assess the taxonomy of Cypriot elephants, and instead focus on the information that *P. cypriotes* can provide on the parallel evolution of dwarfism.

3.2. Geographic isolation of elephants on islands

The geographic distribution of dwarf elephant taxa underpins hypotheses of conspecifity. Because dwarfism in elephants is an insular phenomenon, it is thought to have evolved independently on each island. Thus dwarf taxa on Cyprus evolved in parallel to those on Sicily, and are not considered conspecific, even if they are morphologically similar (a process-based species hypothesis; Chapter 4). Conversely, conspecifity between Maltese and Sicilian dwarf elephants is primarily based on the presumed contiguity of these islands at eustatic low-stands. In practice, therefore, geographic isolation precludes conspecifity (as recognized here; see Chapter 4 for discussion of species concepts). In addition, the extent (both temporal and spatial) of geographic isolation is expected to affect rate and likelihood of immigration, and thus island biodiversity (MacArthur & Wilson 1967), as well as the time available for dwarfism to evolve.

Island	Elephant taxa studied	All localities for included taxa?	Within-island taxonomic revision	Between island comparison
Malta	3/3	Yes	Yes	Yes
Sicily	3/4	No	Partial	Yes
Crete	1/2	Yes	No	Yes
Cyprus	1/2	No	No	Yes
Tilos	1/1	Yes	Yes	Yes

Table 3.1. The impact of site inclusion on hypothesis testing. As exhaustive sampling was only possible on Malta and Tilos, the sites chosen for study on other islands impact on the hypotheses that can be tested, particularly for within-island comparisons. This thesis is thus unable to address the taxonomy and systematics of the 'large-sized' dwarfs on Crete and Cyprus, and the '*P. antiquus*-sized' elephant from Via Libertà, Palermo, Sicily. It is also unable to validate the taxonomic identity of *P. cypriotes* specimens from Cypriot sites other than Imbohary. However, even with non-exhaustive sampling, the selection of sites to maximize sample size and efficiency of data-collection enables comparisons between islands to investigate the parallel evolution of dwarfism.

3.2.1. Eustatic sea-level change

The area of a continental island, and its distance from the mainland, are highly affected by sea-level change. Island biogeographical theory predicts that these two factors will directly impact the ecological covariates implicated as potential drivers of insular dwarfism (e.g. species diversity, resource availability, extinction rate, immigration rate) (Mac Arthur & Wilson 1967). At sea level low-stands, islands are larger and closer to the mainland (and may even be connected by a land-bridge). Extant elephants are good swimmers, and have reportedly swum distances of 48km (Johnson 1980), so the likelihood of a full-sized Pleistocene elephant reaching and becoming isolated on an island is best viewed as a probability function of the islands' distance from the mainland rather than a dichotomous difference between the presence and absence of a land-bridge. All other factors being equal (e.g. prevailing currents; random, probably accidental, 'excursions' into the sea), this should thus vary over time in proportion to the Pleistocene sea-level change curve. I used bathymetric maps of the present day Mediterranean (from www.geomappapp.org, Arko *et al* 2007) and global sea-level change estimation (see below) to assess the impact of sea-level change on geographical isolation for each of my focal islands.

The dynamics of geographical isolation driven by sea-level change depend on (i) the rate of sea-level change, (ii) the magnitude of that change, (iii) the bathymetric profile between the island and the mainland (or between islands for Malta and Sicily). Tectonic movement affecting the relative vertical displacement of mainland, sea floor and island is dealt with below. Mediterranean dwarf elephants are thought to have occurred on islands from the early Middle Pleistocene until the Holocene, encompassing several glacial-interglacial cycles and their concomitant sea-level changes. At the last glacial maximum (LGM), global sea-level was approximately -120m relative to the present day (Lambeck *et al* 2002). This magnitude of drop is in line with global-sea levels reconstructed for earlier glacials from the benthic oxygen isotope records ($\partial^{18}O$) record (Siddall *et al* 2003). The effect of 120m drop in sea level on Mediterranean land-sea boundaries is significant (Figure 3.2). The rate of sea-level change is also thought to have been high, perhaps as much as 1.6m per century, based on data from MIS 5e (Rohling *et al* 2008).

Crete and Cyprus remain islands at maximum sea level drop

Based on current bathymetry, Crete and Cyprus remain isolated from the mainland (Figure 3.2), although the distance to the mainland is reduced, while Sicily, Malta (Figure 3.3) and Tilos do not (Figure 3.4). Mean global sea-level for the past 800 ka was calculated by Prof. Eelco Rohling (National Oceanographic Centre, Southampton) using benthic $\partial^{18}O$ records from Lisieki & Raymo (2005), scaled to reflect global pore-water studies (Adkins *et al* 2002) and normalised to a -120 m sea-level change at the last glacial maximum (Figure 3.4d). This provides an approximate, but reasonable indication of global sea-level (E. Rohling, pers. comm. 2007). Reconstructing past shorelines beyond this level of approximation (global sea-level change, isostasy and local tectonic activity must all be accounted for) is beyond the scope of this thesis.

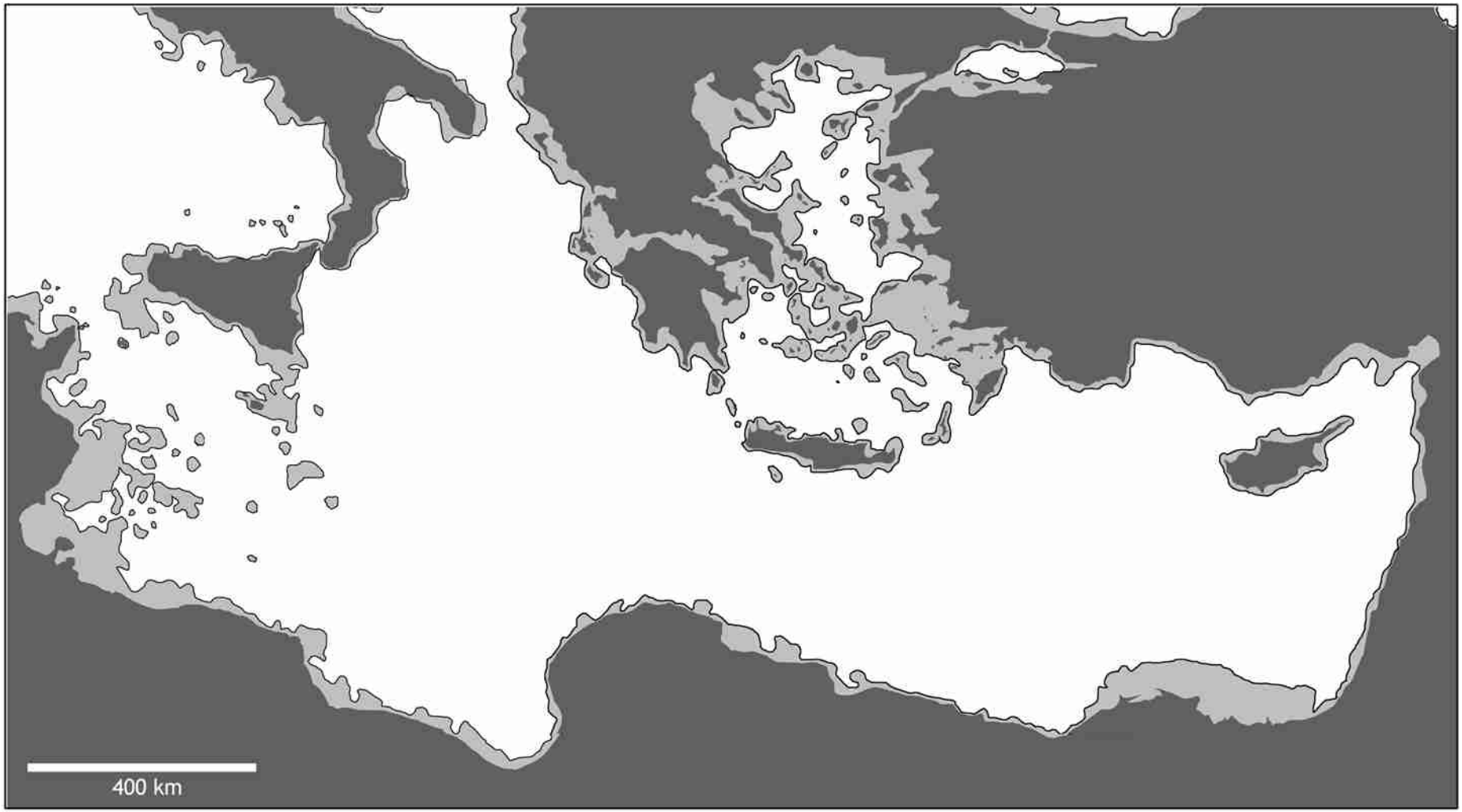

Figure 3.2. The effect of a 120m sea-level drop on Mediterranean coastlines. Current Mediterranean shoreline (dark grey) and predicted shoreline at -120m (light grey). Bathymetric contour information from www.geomappapp.org. Sicily and Malta become contiguous with each other and with mainland Italy. Much of the Dodekanese, including Tilos, form part of a landbridge stretching from mainland Greece to mainland Turkey. Crete and Cyprus remain as islands, although the distance to the mainland is reduced. No allowance is made for tectonic movement.

Malta and Sicily are only contiguous when connected to the mainland

The minimum depth between Malta and Sicily, and between Sicily and the mainland are equivalent, at approximately -110 m (Figure 3.3). A glacial sea-level drop of -110 m is necessary to connect Malta to Sicily, but will also connect Sicily to the mainland: thus a contiguous Maltese-Sicilian landmass is not an insular landmass. Equally, an interglacial sea-level rise that isolates Sicily from the mainland simultaneously isolates Malta from Sicily. If insularity (or its ecological correlates) is the primary driver for the evolution of dwarfism in the elephant taxa on these islands then, based on these data, dwarfism must have occurred in parallel on Malta and Sicily, arguing against their conspecifity. Alternatively, dwarf taxa may have evolved on one of the islands and then colonised the other during a eustatic low-stand. As dwarfism in elephants is only supposed to be adaptive under insular conditions (corroborated by faunal turnover events, see below), the persistence of these colonizers would be unlikely.

For Malta and Sicily to form a palaeo-island at eustatic lowstands, there needs to be a considerable offset between the bathymetrical depth of the Maltese Channel and the Messina Strait. Tectonic evidence suggests that the South-West Sicilian coast is tectonically stable, but that North-East Sicily (and the Messina Strait) is not (Antonioli *et al* 2006). It is therefore possible that the Messina Strait was considerably deeper and wider in the past. Palaeobiogeographical evidence of similar faunal complexes occurring on both islands is seen to support the past existence of a contiguous Sicilo-Maltese region, but the stratigraphies of Malta and Sicily have not been fully integrated. Furthermore, as the synonymy of dwarf elephants, or other endemic fossil taxa, on Sicily and Malta has never, to my knowledge, been systematically verified, these shared faunal complexes may themselves reflect the presumed contiguity between the islands. Proving synonymy is itself problematic if there are no good diagnostic features for a species except those relating to endemic evolution, as parallel evolution may occur (Chapter 4). Until independent, physiographic evidence of an insular Sicily-Maltese region is provided, the *a priori* assumption of conspecifity based on the presumed contiguity of these islands appears inappropriate.

Sicily and Malta have longer isolation times than Tilos

The bathymetry of the Tilos region indicates much shallower water than that surrounding Sicily. Tilos connects to the neighbouring island of Chalki with a -10m drop in sea-level, forming an island approximately three times the size of its current surface area. A drop of around -20m results in a land bridge forming between Tilos and the mainland. Placing the dissimilar bathymetric profiles of Sicily/Malta and Tilos into the context of the apparently rapid sea-level change characteristic of the Quaternary (Figure 3.4 d), the implications for dwarfing hypotheses are apparent: Tilos is characterised by short periods of insularity in the order of 10 ka, whereas on Sicily and Malta insularity continues for approximately 100 ka. When considered in the light of the body-size change observed in Tilos *versus*

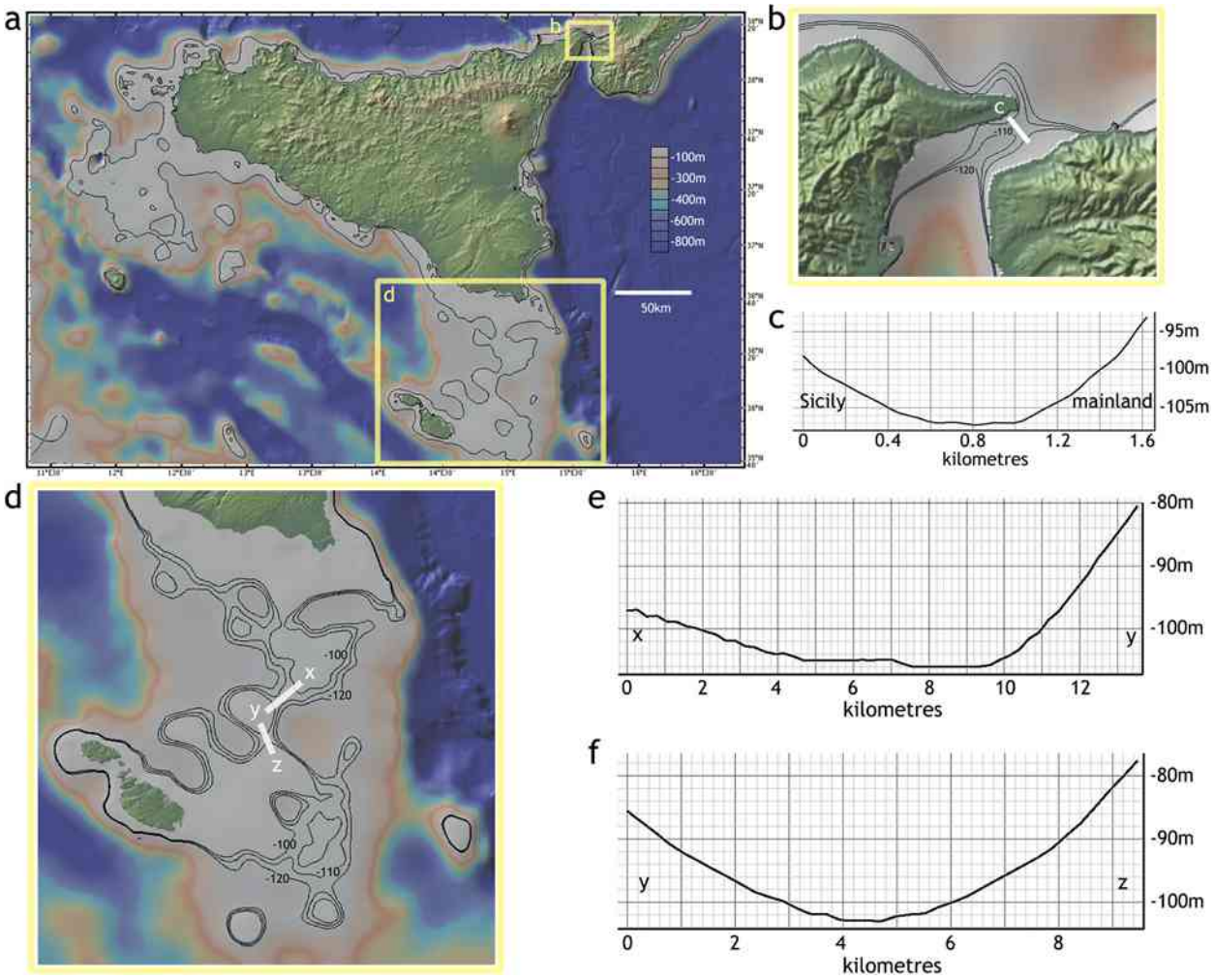

Figure 3.3. Bathymetry of the Sicily/Malta continental shelf. a. Sicily and Malta with -120 m contour. Inset areas b and d indicated. **b.** The Messina Strait, 10m contours drawn between -100 m and -120 m. A cross-sectional bathymetrical profile, **c.** indicates that maximum depth in this region is approximately -107 m**. d.** The Maltese Channel with 10 m contours drawn between -100 m and -120 m. Cross-sectional bathymetrical profiles from **e.** x to y and **f.** y to z indicate that maximum depth is -106 m and -103 m respectively. Thus the sea-level change threshold connecting Sicily to the mainland is similar to that connecting Sicily and Malta to one another: when insular conditions exist on Sicily, they also exist on Malta. White lines indicate where bathymetrical profile was taken.

Sicilian dwarf elephants (Chapters 4 & 6), this suggests that isolation time may have a role to play in the degree of dwarfism evolved.

Constraints on reconstructing sea-level change and bathymetry

The above observations are preliminary, and suffer from three significant constraints. First, the bathymetrical charts are limited in their accuracy and error in continental shelf regions. They are reconstructed from satellite altimetry data which deviates from linear models in areas of high sedimentation (shelf regions), and are affected by sea-surface conditions at the time those data are recorded (Smith & Sandwell 1997). This is particularly problematic for Tilos, where multibeam swath data (an echosounding method used to map bathymetry) is not available to supplement the altimetry base-map (www.geomappapp.org). The -120 m contour map of the Mediterranean produced here (Figure 3.2) is also at odds with an earlier map by Van Andel & Shackleton (1982). Second, the true impact of tectonic activity on sea-floor bathymetry is unknown, and although the general Mediterranean trend is uplift, there is significant evidence for subsidence in the Cretan and Aegean regions (Pe-Piper *et al* 2005). Third, the sea-level reconstructions are based on simple conversion principles (E. Rohling, pers. comm. 2007). Accurate reconstructions have not yet been produced beyond MIS 11 (Siddall *et al* 2003), although they are in progress. Despite this, and acknowledging that current knowledge is not sufficient to reconstruct contemporary island environments with confidence, this approach provides new insights into the geographical factors affecting dwarfism.

3.2.2. Tectonic activity

As previously mentioned, a full review of the local tectonics of each island is beyond the scope of this thesis. Crete and Cyprus had attained their modern dimensions by the beginning of the Pleistocene, and local tectonic activity has had little impact on island surface area or distance from the mainland since then (Pe-Piper *et al* 2005). On Sicily (and thus, by extension, Malta) and Tilos, however, local tectonic uplift and volcanism have been invoked as important factors in the evolution and extinction of dwarf elephants. I discuss these in more detail below.

The Calabrian Arc and the orogeny of Mount Etna

Sicily straddles the African and Eurasian plates: the south-east corner of Sicily (the Hyblean Plateau, which extends to Malta) forms part of the African Plate, and the northern coastline part of the Eurasian Plate. Its tectonic history is complex, and the early Middle Pleistocene of Sicily was characterised by major geomorphological change (Yellin-Dror *et al* 1997, Gvirtzman & Nur 1999, Serpelloni *et al* 2007).

The Hyblean Plateau formed as a result of the collision between the African Plate and the Calabrian Arc, and was supplemented by uplift due to local volcanism. Its uplift stabilised by the Early Pleistocene (Yellin-Dror *et al* 1997). The high-ground of Northern Sicily was initiated in the Late

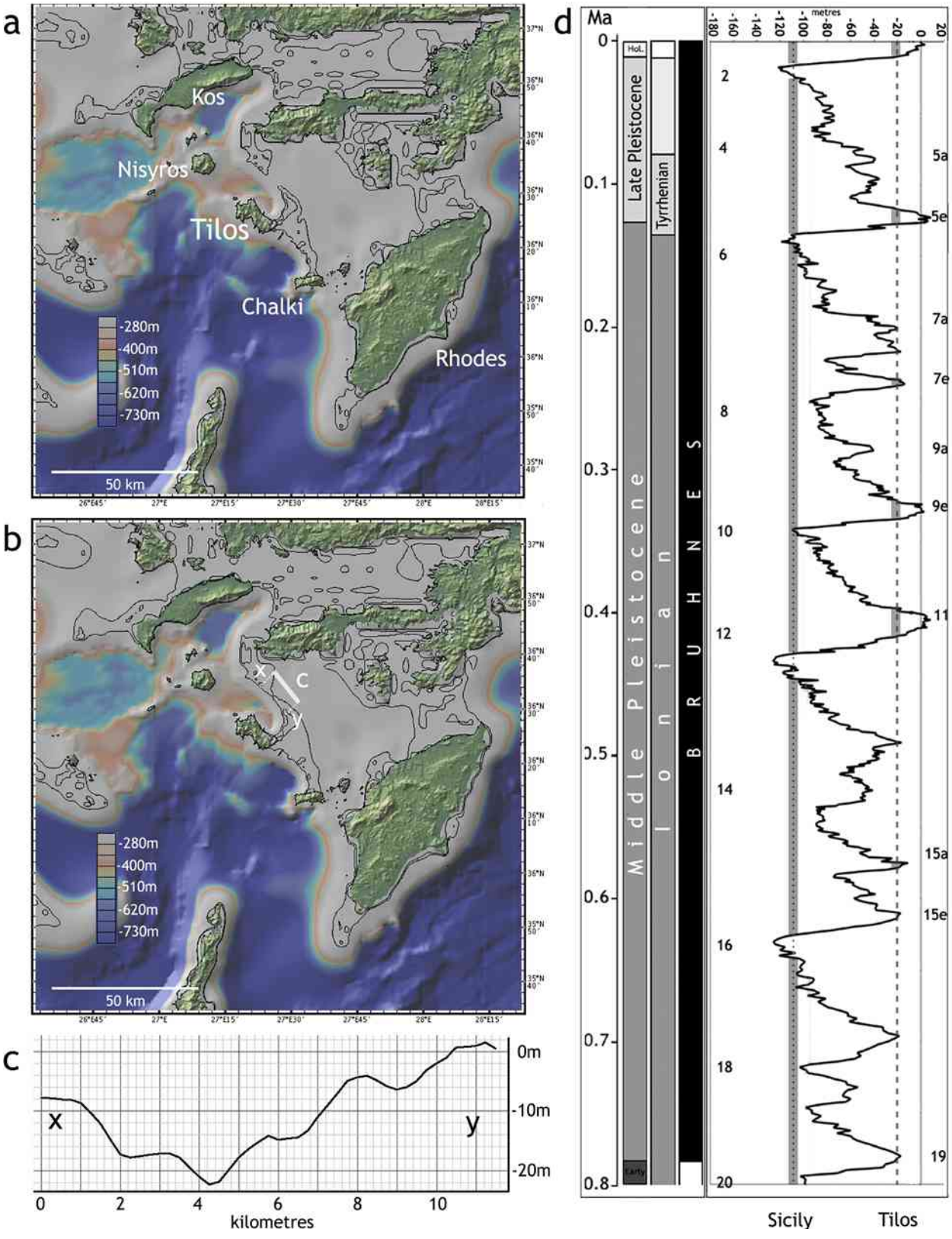

Figure 3.4. Bathymetry of Tilos and surrounding area. a. a -10 m contour joins Tilos and the neighbouring island of Chalki. **b.** a -20 m contour joins Tilos to the mainland. **c.** Bathymetric profile of sea floor between x and y indicates the maximum depth in the region is -21 m. However, there is an unknown level of error in these readings: the profile reads +1 m at y, although this region is currently submerged (see text for discussion). **d.** mean global sea-level change estimated from benthic $\delta^{18}O$ records. Dashed line at -20 m represents the depth at which Tilos becomes connected to the mainland, dotted line at -110 m the depth at which Sicily is connected to both Malta and the mainland. Shaded grey regions on each line highlight periods of insularity. Sicily/Malta are characterised by long periods of isolation and short periods of connectivity to the mainland, while the converse is true for Tilos

Miocene-Early Pleistocene with the opening of the Tyrrhenian Basin, and uplift continues to this day (Serpelloni *et al* 2007). Mount Etna, which occupies the central east coast region of Sicily between the Hyblean Plateau and Northern Sicily, began to form at around the same time as major uplift occurred in the Calabrian Arc, 700-500 ka, but the majority of Etna's orogeny occurred in the last 200 ka (Gvirtzman & Nur 1999). It was not until some time in the Middle Pleistocene that the northern and south-eastern regions of Sicily formed a single land mass - before then they were separate islands in a larger Calabrian Archipelago (Figure 3.5)

Bonfiglio *et al* (2002, p.34) argue that the impoverished and highly endemic fauna of the '*E. falconeri* Faunal Complex (FC)' on Sicily (see below) suggests the occurrence of 'strongly geographically isolated small islands', and correlate it with the physiographic evidence for the Early-Middle Pleistocene archipelago denoted in Figure 3.5. If so, this has ramifications for the validity of Sicilian *P. falconeri*, which is found in large numbers at Spinagallo Cave (on the Hyblean Plateau) and at Luparello Cave (Northern Sicily) (Figure 3.2). Under this scenario, these localities were on separate islands, and the dwarf elephant populations may therefore have evolved independently on each of them. Even more complex scenarios could be envisaged, wherein Sicilian *P. falconeri* evolved on one such island and subsequently expanded to the rest of Sicily once a land connection was established. Or, potentially, parallel evolution of dwarfism in each region, followed by interbreeding between the closely related and similar-sized taxa after the islands became connected, re-introducing the complex issue of species concepts to dwarf elephant systematics. The timing of the formation of 'modern' Sicily and the age of *P. falconeri* on Sicily need to be resolved (see section 3.4.1) to allow this palaeogeographic scenario to be explored further, particularly as comparisons of dwarf elephant dental morphology indicate that some differences exist between Luparello and Spinagallo Cave populations (Chapter 6).

Aegean Volcanism

Tilos is situated at the western edge of the Aegean Arc, a region characterized by Quaternary volcanic activity (Pe-Piper *et al* 2005). The timing of the formation of this island is unclear; however, marine sediments off the west coast of Tilos have been dated to 0.5 Ma and volcanic tuff deposits in central Tilos are correlated with the Kos Plateau Tuff (161 ka) (Pe-Piper *et al* 2005), suggesting a Middle Pleistocene age. The Pleistocene faunas of Tilos are not thought to have been greatly affected by the tectonic history of the island, beyond, of course, its origin (Theodorou 1988), but are instead argued to have been affected by the volcanic activity of the neighbouring islands of Kos and Nisyros (Figure 3.4.).

The largest volcanic event of the Quaternary Aegean Arc is thought be the KPT eruption at 161 ka. A hundred cubic kilometers of ash and pumice was deposited over a 2000 km^2 area, including Tilos, several other Dodecanese islands and the Turkish mainland (Keller *et al* 1989), and there is evidence of pyroclastic flows crossing large stretches of open sea (Keller *et al* 1989, Pe-Piper *et al* 2005). After this major catastrophic event, the formation of the island of Nisyros (a caldera volcano) was accompanied by

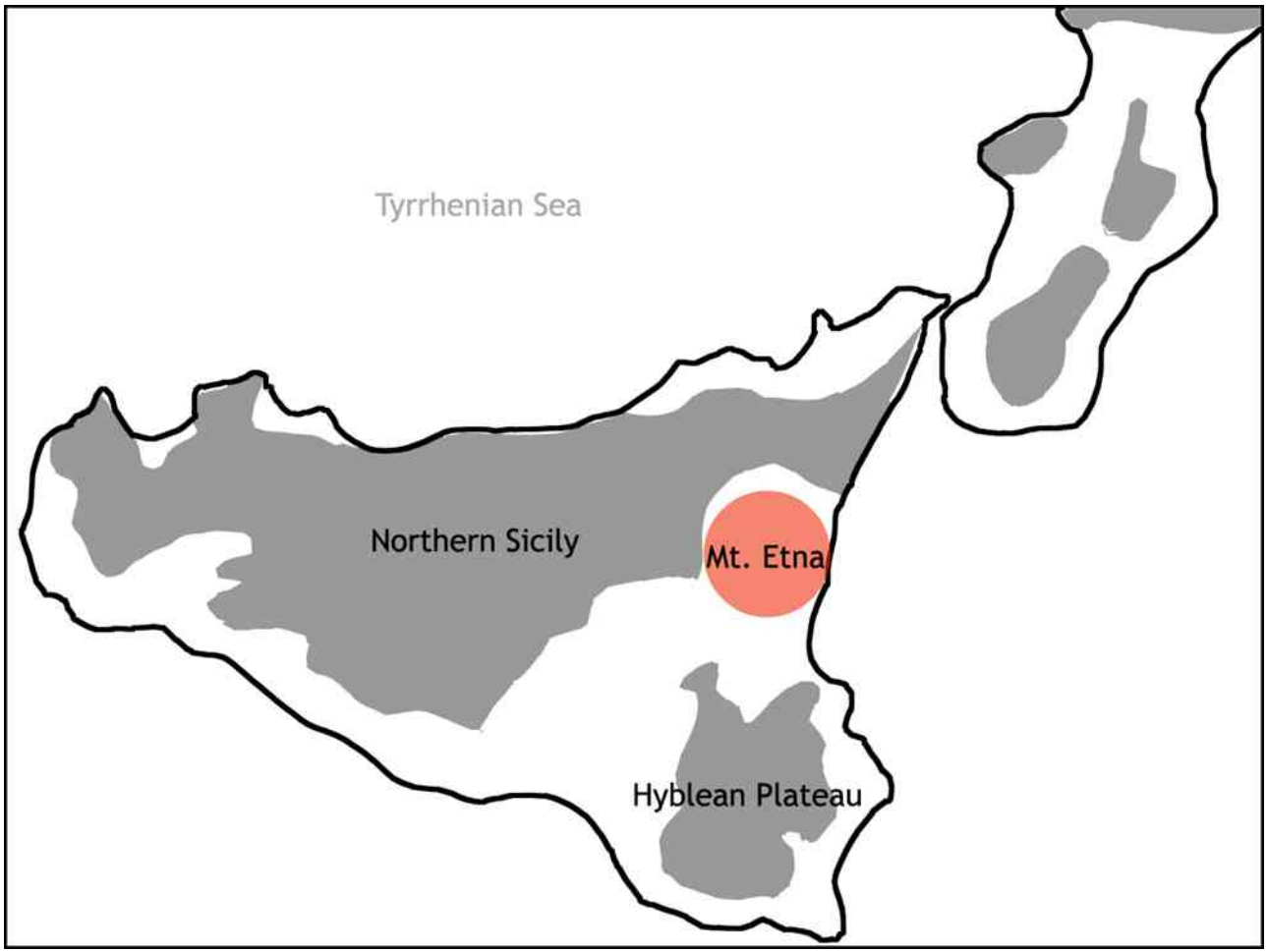

Figure 3.5. Geomorphological evolution of Late Pliocene to Middle Pleistocene Sicily and Calabria. The modern outline of Sicily and the Southern Italian Penninsula (black outline) was in place by the Late Pleistocene. Northern Sicily and the Hyblean Plateau formed part of a Calabrian archipelago (grey shading), uplifted during the Early to Middle Pleistocene. The orogeny of Mt. Etna (red shading) began at approximately 700 ka, along with uplift in the Calabrian Arc, but the bulk of its formation occurred approximately 200 ka (Gvirtzman & Nur 1999). The Hyblean Plateau, Northern Sicily and the region of MT. Etna were joined into a single island at some point in the Middle Pleistocene, but the timing of this is unconfirmed. Map modified from Bonfiglio *et al* (2002).

12 pyroclastic eruptions between 66 ka and 24 ka, collectively known as the Kyra Sequence, six of which have been correlated with deposits on Tilos, as well as more recent eruptions into the Holocene.

Theodorou (1988) argues that these catastrophic events played an important role in faunal extinction and turnover, suggesting that as a small island already limited in water and food resources, Tilos would have become uninhabitable following the deposition of substantial amounts of ash. He postulates that the early, slightly endemic deer population went extinct following the KPT event, and that the major eruption of Santorini at 3.5 ka may have played a contributing factor in the final extinction of elephants on Tilos (Theodorou 1988).

Tuff has been recorded in Charkadio Cave sediment associated with the deer and elephant layers (section 3.4.4, Appendix A1.5) but the exact nature of the correlation between the tuff in these layers and the KPT or Kyra Sequence is unclear, and there are conflicting interpretations (Theodorou 1988, Hujer *et al* 2008). Other dating methods for Charkadio Cave material are disputed (see below), it is therefore not currently possible to show a clear correspondence between local volcanic events and faunal turnover, and the effect of volcanism on Tilos must be treated as a plausible hypothesis only. Nevertheless, this hypothesis adds an interesting layer of complexity to the dynamics of the Quaternary environment and its impact on elephant evolution, and also raises questions for Cretan elephant evolution and extinction that could have been affected by the multiple eruptions of Santorini over the last 200 ka (Keller *et al* 1989).

3.3. Dating dwarf elephant fossils and horizons

Four different methodologies have been employed to date the occurrence of Mediterranean dwarf elephants: (i) radiocarbon (^{14}C) dating, (ii) electron spin resonance (ESR) dating, (iii) amino-acid racemisation (AAR) dating and (iv) Uranium-series dating. Radiocarbon, ESR and AAR methods are used to date fossils directly, whereas U-series has been more usually employed to date speleothems in clear stratigraphical relation with fossiliferous material, providing a minimum and/or maximum age constraint for that material. Each geochronological tool has a different, inherent level of precision and/or accuracy, as well as a restricted time-span of 'usefulness', within which its precision and accuracy can be relied upon. These limits are revised and refined as technological and methodological advances are made, often discrediting the results from earlier analyses (e.g. Blackwell *et al* 1990, Pettitt *et al* 2003, Jacobi *et al* 2006). AAR and ^{14}C approaches were in their infancy when they were used to date elephant fossils in the 1980s, and the reliability of these dates is questionable. Despite this, published dates continue to be frequently cited, used to calibrate biostratigraphical correlations (Bonfiglio *et al* 2002, Poulakakis *et al* 2002a, Marra 2005), estimate evolutionary rate (Millien 2006) or support evolutionary hypothesis (Mol *et al* 1996, Poulakakis *et al* 2002a, Poulakakis *et al* 2006). Below I assess the reliability of these dates. In the following section I evaluate their usefulness for understanding dwarf elephant evolution.

3.3.1. ^{14}C dating

^{14}C dating is a radiometric technique based on the radioactive decay of ^{14}C to ^{14}N (half-life = 5730 ± 40 years), with a background limit of approximately 55 ka (Walker 2005, Jacobi *et al* 2006). Its accuracy depends on a number of assumptions: (i) that atmospheric ^{14}C levels are constant, or known, through time; (ii) that atmospheric levels are in equilibrium with the incorporation of ^{14}C into organic tissue; (iii) that ^{14}C concentration in a fossil reflect the radioactive decay of this element since time of death (it is a closed system) (Walker 2005).

Early work established that atmospheric levels of ^{14}C were not constant through time (violating assumption (i)), and highlighted a need for 'calibrated' ^{14}C years. Calibrated ^{14}C years correct for variation in atmospheric ^{14}C levels, based on the correlation between the ^{14}C date of a sample, and another independently calculated date for the same sample (e.g. dendrochronology or U-series dates from corals). The radiocarbon calibration curve has now been extended to 50 ka, in line with the upper limit of ^{14}C dating (Reimer *et al* 2009); all ^{14}C dates published for dwarf elephants are uncalibrated.

Assumption (ii) is widely accepted for terrestrial herbivores, and does not affect the reliability of dates made directly on dwarf elephant tissue. Reservoir effects may impact on marine- or riverine-derived samples, however, leading to an overestimation of age (Simmons *et al* 1989). The assumption that bone acts a closed system is frequently violated, and contamination of samples by younger ^{14}C is a real problem (Walker 2005). The major advances in radiocarbon methodology in recent years have addressed this issue of post-depositional contamination, using ultra-filtration methods to extend the reliability of ^{14}C dating to ca. 55ka (Higham *et al* 2006, Jacobi *et al* 2006). ^{14}C dates greater than ~ 35-40 ka that are published without following this method are not considered reliable, and it has been suggested that all dates published prior to 1990 should be treated with caution (Jacobi *et al* 2006).

All ^{14}C dates published relating to dwarf elephant localities pre-date 1990, and did not use an ultra-filtration methodology. In this study I employ the quality assessment protocol designed by Pettitt *et al* (2003) to rate the reliability of existing dates (Tables 3.2 & 3.3). I then consider this assessment alongside other information, including authors' comments on the reliability of the results, subsequent ^{14}C dating attempts and independent corroboration of dates, to evaluate reliability (Table 3.4.).

Assessing the reliability of published ^{14}C dates

Pettitt *et al* (2003) propose a 36 point scheme, summarized in Table 3.2, where dates are given a score of 0-4 for nine different 'reliability criteria'. One of these is explicitly designed to assess confidence of coeval human presence, and is thus ignored for my purposes. The summation of scores in each category therefore produces a total out of 32, which can be interpreted by converting the absolute scores to percentages, and comparing these with similarly converted scores from Pettitt *et al* (2003). A score less than 25% indicates a highly unreliable date, while 75% can be treated as reliable. Any date with an intermediate score (25-75 %) should be treated with caution. Where there was insufficient published detail to definitively score a sample for a particular category, the possible range of scores was recorded

Table 3.2. Assessing the reliability of pre-1990 ^{14}C dates: Tilos and Crete. ^{14}C dates for Tilos and Crete were scored following the assessment criteria of Pettitt *et al* (2003). The criteria are numbered here following their scheme to allow cross-comparison. The 0-4 scoring categories are summarized by me. Dates are assessed separately for each identifiable stratigraphic unit or horizon.

Pettitt *et al* (2003)		0	1	2	3	4	Island	Tilos			Crete
							Reference	Bachmayer *et al* (1984)		Bachmayer & Symeonidis (1975)	Bachmayer & Zapfe (1985)
							Site/trench [horizon]	Charkadio Cave I [0.6m]	Charkadio Cave I [3.6m]	Charkadio Cave II	Katharo Basin
							Uncalibrated age	17k +1.9 a -1.5	35k ±0.6 45k +3.1 a -2.2	4.4ka ±0.6 7.1ka ±0.7	12ka ±0.5
3.1.1	**Contamination**	burnt bone	not enough C to evaluate C/N	unknown conservation history	unproblematic pre-treatmet	C from bone-specific AA		1-3	1-3	1-3	1-3
3.1.2	**Multiple fractions**	1 material, no stratigraphy	1 material, cannot cross-check horizon	1 material, fall in sequence	2(+) bone samples per horizon, same age	several bone samples & charcoal, same age		2	2	1	1
3.1.3 .	**Accuracy**	one sample, >30ka	2+ samples, >30ka, few outliers	2+ samples, >30ka, no outliers	<30 ka, clear chronological sequence	<20 ka, clear chronological sequence		0	1	4?	0
3.1.4	**Materials/ ^{14}C method**	riverine/marine sample not corrected for reservoir effect	carbon yield very low	collagen and/or carbon yield low	good collagen yield	good collagen yield, same age as rest of horizon		? 0-4	? 0-4	? 0-4	? 0-4
3.1.5	**Measurement & reporting**	bulk sample, pre 1970	measured at non-IRLI lab	no published info	some published criteria outside acceptable limits	fully published, best-practice		2	2	2	2
3.2.2	**Association**	unknown sample material	no published association exists	sample in same horizon	high prob. association	sample directly dated		4	4	4	1
3.2.3	**Dates per horizon**	1 date/many sig. dif. dates	2 dates, not sig. dif,	2+ dates, not sig. dif.	3+ dates, not sig. dif.	5+ dates, not sig. dif.		0	0	1	0
3.2.4	**Stratigraphic mobility**	small bone fragment	<10cm max dimension, no stratigraphic integrity	<10cm max dimension, clear stratigraphic integrity	>10cm max dimension, clearly stratified	>10cm, articulated skeleton		2-3	2-3	2-3	2-3
							Total (Min)	11 [34%]	12 [38%]	15 [47%]	7 [21%]
							Total (Max)	18 [56%]	19 [60%]	20 [62%]	14 [44%]
							Assessment	**CAUTION**	**CAUTION**	**CAUTION**	**CAUTION**

(e.g. no information would give a score of 0-4), and both the minimum and maximum final scores were calculated. The maximum total score therefore provides a 'generous' index of reliability of the date; if this falls below the reliability threshold of 75%, the date should be treated with scepticism. Across the board, published radiocarbon dates for Tilos and Crete (Table 3.2) and for Akrotiri Aetokremnos (Table 3.3) were assessed as having low reliability, and should be treated with caution (Table 3.4).

3.3.2. AAR dating

In life, an organism's constituent amino acids exist as L-configuration isomers. After death, interconversion between L-isomers and D-isomers occurs, and continues until an equilibrium ratio of 1:1.30 between the two chiral forms is reached (Miller & Mangerud 1985). This process is known as 'racemisation'. AAR geochronology treats the post-mortem increase in the proportion of D-isomers as a function of time (and temperature), and thus the ratio of D/L amino acids in a sample can provide an estimate of time since death.

AAR dating has sometimes been referred to as an absolute dating method (e.g. Reese *et al* 1996), but this is a misnomer: unlike radiometric techniques, it is a chemical reaction, and therefore there is no universal or intrinsic rate at which amino acids racemize. To produce an 'absolute' date, racemisation rate has to be estimated using an independently dated, preferably paired, sample for calibration. The validity of this calibration date, as well as the applicability of calculated racemisation rates to other samples at the same site, or nearby, underpin the validity of the calculated AAR 'absolute' age. If these are problematic, then, at best, AAR is a relative dating tool within a narrowly defined locality, though its efficacy for this has also been questioned (Blackwell *et al* 1990).

Racemisation rate is a function of temperature, as well as time, and can vary between localities (Clarke & Murray-Wallace 2006). Moreover, with the glacial-interglacial fluctuations of the Quaternary, this temperature-dependent racemisation rate is unlikely to have been constant through time. Different taxa have been shown to have varying racemisation rates, and the depositional environment (e.g. pH, water circulation) can impact on amino acid diagenesis and leaching, violating closed system assumptions (Clarke & Murray-Wallace 2006, Walker 2005).

Blackwell *et al* (1990) reviewed the methodology as it was then implemented, showing that the method was inaccurate and lacked precision, regardless of the rate constant employed, and concluded that AAR dating should not be applied to Middle Pleistocene bones and teeth (these tissues seemed most susceptible to diagenetic effects). There have been recent advances in AAR methodologies for mollusc shells (Penkman 2009) which herald an increase in the usefulness of this method. All AAR dates published for dwarf elephants pre-date these methodological improvements, and are based on enamel.

Dwarf elephant AAR dates are, however, widely cited (e.g. Bonfiglio *et al* 2002, Poulakakis *et al* 2002b, Marra 2005, Palombo & Ferretti 2005, Raia & Meiri 2006). A number of important claims rest upon these dates, including validation for the earliest human occupation of Cyprus and the age of one of

Provenance	Sample	Age (years)	Pettitt *et al* (2003) criteria								Total (min)	Total (max)	Assessment
			3.1.1	3.1.2	3.1.3	3.1.4	3.1.5	3.2.2	3.2.3	3.2.4			
Surface	bone collagen (*Phanourios*)	3700 ±60	0	0	3	1-3	2	2	3	0	11 [34%]	13 [41%]	**CAUTION**
	burnt bone (*Phanourios*)	6310 ±160	0	0	3	1-3	2	2	3	0	11 [34%]	13 [41%]	**CAUTION**
	burnt bone (*Phanourios*)	8330 ±100	0	0	3	1-3	2	2	3	0	11 [34%]	13 [41%]	**CAUTION**
Stratum 2	humins fraction	9240 ±420	0	1	3	1	2	2	4	0-2	13 [41%]	15 [47%]	**CAUTION**
	soil, bulk org. carbon	9490 ±120	0	1	3	2-4	2	2	4	0-2	14 [44%]	18 [56%]	**CAUTION**
	humic acid	10150 ±130	0	1	3	1	2	2	4	0-2	13 [41%]	15 [47%]	**CAUTION**
	charcoal	10190 ±230	1-2	1	3	0	2	0	4	0-2	11 [34%]	14 [44%]	**CAUTION**
	charcoal	10420 ±85	1-2	1	3	0	2	0	4	0-2	11 [34%]	14 [44%]	**CAUTION**
	charcoal	10480 ±300	1-2	1	3	0	2	0	4	0-2	11 [34%]	14 [44%]	**CAUTION**
	charcoal	10485 ±80	1-2	1	3	0	2	0	4	0-2	11 [34%]	14 [44%]	**CAUTION**
	charcoal	10575 ±80	1-2	1	3	0	2	0	4	0-2	11 [34%]	14 [44%]	**CAUTION**
	charcoal	10770 ±80	1-2	1	3	0	2	0	4	0-2	11 [34%]	14 [44%]	**CAUTION**
	shell	10800 ±110	1-2	1	3	0	2	2	4	0-2	13 [41%]	16 [50%]	**CAUTION**
	charcoal	10840 ±270	1-2	1	3	0	2	0	4	0-2	11 [34%]	14 [44%]	**CAUTION**
	shell	10970 ±100	1-2	1	3	0	2	2	4	0-2	13 [41%]	16 [50%]	**CAUTION**
	shell	11000 ±100	1-2	1	3	0	2	2	4	0-2	13 [41%]	16 [50%]	**CAUTION**
	shell	11030 ±500	1-2	1	3	0	2	2	4	0-2	13 [41%]	16 [50%]	**CAUTION**
	shell	11200 ±500	1-2	1	3	0	2	2	4	0-2	13 [41%]	16 [50%]	**CAUTION**
	charcoal	11720 ±240	1-2	1	3	0	2	0	4	0-2	11 [34%]	14 [44%]	**CAUTION**
Strata 2/4	bone apatite (*Phanourios*)	9040 ±160	0	1	3	1	0	2	4	0-2	11 [34%]	13 [41%]	**CAUTION**
	bone org. fraction (*Phanourios*)	9100 ±790	1-2	1	3	1	0	2	4	0-3	12 [38%]	16 [50%]	**CAUTION**
	burnt bone (*Phanourios*)	9250 ±150	0	1	3	2-4	2	2	4	0-3	14 [44%]	19 [63%]	**CAUTION**
	shell	10810 ±110	1-2	1	3	0	2	0	4	0-2	11 [34%]	14 [44%]	**CAUTION**
	shell	10840 ±60	1-2	1	3	0	2	0	4	0-2	11 [34%]	14 [44%]	**CAUTION**
Stratum 4	burnt bone (*Phanourios*)	7150 ±140	0	1	3	2-4	2	2	4	0-3	14 [44%]	19 [60%]	**CAUTION**
	shell	7900 ±500	1-2	1	3	0	2	2	4	0-2	13 [41%]	16 [50%]	**CAUTION**
	shell	10100 ±370	1-2	1	3	0	2	2	4	0-2	13 [41%]	16 [50%]	**CAUTION**
	charcoal	10575 ±80	1-2	1	3	0	2	0	4	0-2	11 [34%]	14 [44%]	**CAUTION**
	burnt bone (*Phanourios*)	10770 ±160	0	1	3	2-4	2	2	4	0-3	14 [44%]	19 [60%]	**CAUTION**
	shell	11200 ±130	1-2	1	3	0	2	2	4	0-2	13 [41%]	16 [50%]	**CAUTION**

Table 3.3. Assessing the reliability of pre-1990 ^{14}C dates: Cyprus. ^{14}C dates for Cyprus from Reese (1995) and Simmons (1989) were scored following the assessment criteria of Pettitt *et al* (2003). The criteria are numbered here following their scheme (summarized in Table 3.2) to allow cross-comparison. Dates are assessed separately for each identifiable stratigraphic unit or horizon

	Tilos	Crete	Cyprus	Cyprus
	Charkadio Cave (all)	Katharo basin	Ak. Aetokremnos (surface)	Ak. Aetokremnos (Str. 2-4)
Sample	*P. tiliensis* bone?	*Hippopotamus* bone	*Phanourios* bone	*Phanourios* bone, shell & charcoal
Association	direct	biostratigraphically younger	same stratum	same stratum
Petitt *et al* (2003)	treat with caution	treat with caution	treat with caution	treat with caution
Author comments	-	possibly deficient[1]	contaminated[2]	-
Ultra-filtration?	No	No	No	No
post-1990 sample failure?	Yes[3]	-	-	Yes[4]
Independent age estimate/corroboration	Yes/Partial	Yes/No	No[5]	No[5]
Reliability	**LOW**	**LOW**	**VERY LOW**	**LOW**

Table 3.4. Reliability of ^{14}C dates for dwarf elephant and hippo localities. 1. H. Zapfe, pers. comm. to Reese *et al* (1996). 2. Simmons (1989) and Reese (1995). 3. A. Lister, pers. comm. (2007) 4. A. Simmons, pers. comm. to A. Lister (2007). 5. AAR dates are not independent – they are calibrated to this site based on these ^{14}C dates. ? indicates inferred information.

the ‘oldest pieces of aDNA ever retrieved’ (Poulakakis *et al* 2006). Beyond the general issues highlighted above, if these dates are to continue to be used, specific criticisms and amendments need to be made. Two key areas should be addressed: (i) racemisation rate calibration, applicable to all sites, dealt with in Appendix 3, and (ii) the selective use of published dates, which is dealt with later on an island-by-island basis (section 3.4). It should be stressed that amendments to rate calibrations presented here (Appendix X), and the subsequent revised dates (Table 3.5) are done within the methodological framework of the original publications, despite the recognized flaws in the methods as they were used at that time. My rationale for doing this, instead of discounting the dates altogether, is to both highlight the inherent error in taxonomic arguments based on absolute dates (discussed in section 3.4), and to provide a small improvement on those dates in light of recent revisions to the age of the main calibration site Isernia La Pineta (Coltorti *et al* 2005).

These revised dates differ from the published ones by up to 100 ka, although relative ages do not change. It should also be noted that Akr. Aetokremnos (Cyprus) alle/ile values are similar to those from Puntali Cave (Sicily), yet their AAR ages are an order of magnitude different (Table 3.5). This difference is entirely due to the choice of calibration date, indicating that racemisation rate is not the same at Isernia La Pineta and Akr. Aetokremnos, and that Mediterranean-wide generalizations of racemisation are inappropriate, even when temperature effects are accounted for. AAR dates associated with dwarf elephants are thus best treated as an indicator of relative geochronolgy, only applicabile within an island where there is a greater chance of similar thermal history. However, as AAR dating on tooth enamel requires further validation, they must be treated with caution even in this respect (Kirsty Penkman, pers, comm.).

3.3.3. ESR dating

Electron spin resonance dating directly measures the trapped electrons which accumulate over time in the crystal lattice of materials (Walker 2005). External radiation sources (e.g. uranium in the sediment, but also cosmic radiation) excite electrons from their ground state to a higher energy level. On returning to their ground state, some electrons become trapped at ‘deficit sites’, becoming paramagnetic centres. The number of trapped electrons is proportional to the radiation dose rate and the time since paramagnetic centre formation (which in tooth enamel is when the enamel is laid down) (Grün 1989). The accuracy and precision of the method are dependent on being able to model the radiation dose rate, and measurements of local radiation levels as well as the uranium levels inside a specimen must be taken to assess this (Walker 2005). In addition, a model of uranium uptake is needed. Typically two models are used: early uptake (EU) and late uptake (LU) (Grün 1989).

While it cannot be determined *a priori* which model is more appropriate, and the ‘true’ age lies somewhere between the age estimates provided by these models, LU models have been shown to more closely approximate independent age estimates of a sample (Grün 1989). Tooth enamel can be dated

Site	Species	Sample	alle/ile	Calibration site	Reference	Published Age (ka)	Recalc. Age 1 (ka)	Recalc. Age 2 (ka)
Sicily								
Spinagallo Cave	*P. falconeri*	enamel	0.26	Isernia La Pineta	Belluomini & Bada (1985)	550 ±138	460 ±92	35 ±7
Luparello Cave	*P. falconeri*	enamel	0.21	Isernia La Pineta	Bada *et al* (1991)	455 ±90*	370 ±74	28 ±6
San Teodoro Cave	*'P. mnaidriensis'*	enamel	0.21	Isernia La Pineta	Bada *et al* (1991)	455 ±90*	370 ±74	28 ±6
Puntali Cave	*'P. mnaidriensis'*	enamel	0.08	Isernia La Pineta	Belluomini & Bada (1985)	180 ±45	142 ±28	11 ±2
Puntali Cave	*H. pentlandli*	enamel	0.11	Isernia La Pineta	Bada *et al* (1991)	200 ±40*	195 ±39	15 ±3
San Teodoro Deposit	*H. pentlandli*	enamel	0.08	Isernia La Pineta	Bada *et al* (1991)	200 ±40*	142 ±36	11 ±2
Crete								
Katharo Basin	*Hippopotamus*	enamel	0.30	Isernia La Pineta	Reese *et al* (1996)	473 ±95	401 ±80	30 ±6
Katharo Basin I	*Hippopotamus*	enamel	0.24	Isernia La Pineta	Reese *et al* (1996)	378 ±76	320 ±64	24 ±5
Katharo Basin II	*Hippopotamus*	enamel	0.45	Isernia La Pineta	Reese *et al* (1996)	687 ±137	611 ±122	45 ±9
Katharo Basin III	*Hippopotamus*	enamel	0.46	Isernia La Pineta	Reese *et al* (1996)	738 ±148	625 ±125	46 ±9
Katharo Basin IV	*Hippopotamus*	enamel	0.35	Isernia La Pineta	Reese *et al* (1996)	554 ±111	469 ±94	35 ±7
Cyprus								
Akr. Aetokremnos, Str. 2	*Phanourios*	enamel	0.10[§]	Akr. Aetokremnos	Reese (1995)	10 ±2	133 ±17	- -
Akr. Aetokremnos, Str. 4b	*Phanourios*	enamel	0.07	Akr. Aetokremnos	Reese (1995)	7 ±1	94 ±18	- -
Akr. Aetokremnos, Str. 4b	*'Elephas'*	enamel	0.13	Akr. Aetokremnos	Reese (1995)	13 ±3	173 ±35	- -

Table 3.5. AAR dates for dwarf elephant localities and the impact of calibration. Published dates for Sicily and Crete are underpinned by the age of deposits at Isernia La Pineta, which has recently been revised to 600 ka (Coltorti *et al* 2005). Dwarf elephant dates must also be amended (Recalc. Age 1, see Appendix 2 for details of recalculation). * 'Group' averages were published for Sicily (Bada *et al* 1991), my recalculations are based on the individual alle/ile ratios for each site. Cyprus AAR dates are underpinned by the ^{14}C dates from Akr. Aetokremnos. Recalc. Age 2 uses k_{iso} fof Akr. Aetokremnos to recalculate AAR ages for Sicily and Crete, demonstrating the significant impact on absolute age choice of calibrator can have. All recalculations take account of temperature effects, following Bada & Belluomini (1985) and Reese *et al* (1996). **§** this alle/ile ratio was used for the calculation of k_{iso}; published ratio is 0.010, but calculated ages for other Cyprus dates (Reese 1995) indicate that this is a typo, and should read 0.10. If not, other Cypriot ages are out by a factor of 10 – i.e. 0.07 is 70 ka rather than 7 ka. Errors are calculated at ± 20% following Bada *et al* (1991) and Reese *et al* (1996). Recalc. is recalculated

directly by ESR methods (Grün 1989, Blackwell *et al* 1992), but because local dose rate must be measured directly from the sediments surrounding a sample, *ex situ* samples can only provide a very broad age estimate, and have little use beyond a range-finder technique (E. Rhodes, pers. comm. 2007). The reliability of ESR dates for dwarf elephants is assessed on the published information (Tables 3.6-3.8) relating to dose rate, uranium concentration and uranium uptake model used (Table 3.9).

Contrada Fusco, Eastern Sicily, is the only Sicilian site for which ESR dating has been used. The elephant material from here was unavailable for study, but it has been biostratigraphically correlated (by the presence of '*P. mnaidriensis'*, *H. pentlandi* and its avifauna) to the '*E. mnaidriensis* FC'. The ESR ages for '*P. mnaidriensis'* and *H. pentlandi* tooth enamel give an EU mean of 88.2 ka and an LU mean of 146.8 ka for the site (Rhodes 1996; Table 3.6). ESR mean ages for different stratigraphic levels are also consistent with the site stratigraphy; however, given the disparity between models and uranium levels, a site mean is more appropriate (Rhodes 1996). Unlike the ESR dates from Crete and Cyprus, these are published with all the necessary information (dose rate, uranium levels and the use of two different uranium uptake models) to render them reliable and fairly precise.

The precision and accuracy of ESR dates published for Katharo Basin (Table 3.7) is qualified by Reese *et al* (1996, p.47) as 'only suggest[ing] the order of magnitude'. Given that this statement is at odds with the precision possible for an appropriately sampled ESR date (Grün 1989, Rhodes 1996), and the corresponding lack of supporting information concerning dose rate, uranium levels or uranium uptake models in Reese *et al* (1996), I speculate that these dates were produced from *ex situ* samples. It is also possible that this caution reflects the great antiquity of the dates returned: conventional ESR is known to have limited use beyond 300 ka (E. Rhodes, pers. comm. 2007). Katharo ESR dates (475.6 ka – 846.0 ka; Table 3.7) must thus be treated as low reliability and low precision. However, they do provide a small amount of independent support for the AAR dates for Katharo Basin, as both are of the same order of magnitude.

As with the Cretan material, there is no published information regarding the dose rates, uranium levels or uptake models for Cypriot ESR dates (Reese 1995). Given that the dates were produced by the same lab as the Cretan ESR dates (Osaka, Japan), it seems to prudent to also treat the Cypriot ESR dates as indicative of the order of magnitude. The very old date for Asproyi is above the 300 ka threshold for conventional ESR dating. By treating it as only indicative of the order of magnitude of the age of the sample, the lower age range (in the 100 ka region) is consistent with the maximum age of another *Phanourios* site, Ayios Phanourios, whose deposits occur on a marine terrace correlated with the Eemian (Reese 1995). The ESR ages in the 10-20 ka age range provide independent corroboration of the AAR dates from the same sites (Table 3.8) and thus support the calibration of those AAR dates to Akr. Aetokremnos. In turn this corroborates the Akr, Aetokremnos ^{14}C dates.

Sample	Species	Level	EU Age (ka)		LU Age (ka)	
SR8a	*H. pentlandi*	L2	115.1	±9.0	179.0	±13.2
SR8b	*H. pentlandi*	L2	109.6	±7.9	167.8	±11.3
SR10	*H. pentlandi*	L2	72.3	±6.1	126.3	±10.2
SR3a	*H. pentlandi*	L2	58.3	±3.8	94.8	±5.9
SR3b	*H. pentlandi*	L2	63.9	±4.2	102.1	±6.3
SR3c	*H. pentlandi*	L2	56.1	±3.4	92.1	±5.0
SR9a	*H. pentlandi*	L2	125.0	±6.8	178.9	±9.7
SR9b	*H. pentlandi*	L2	102.7	±6.2	153.8	±9.0
L2 mean			**87.9**		**136.7**	
SR2a	*H. pentlandi*	C4	105.0	±6.3	163.4	±9.3
SR2b	*H. pentlandi*	C4	99.7	±5.6	157.4	±8.0
SR7	*H. pentlandi*	C4	68.5	±5.0	121.0	±8.3
C4 mean			**91.1**		**147.3**	
SR4a	*'P. mnaidriensis'*	All (East Sector)	89.2	±9.7	161.4	±17.3
SR4b	*'P. mnaidriensis*	All (East Sector)	84.0	±7.8	151.4	±13.9
SR5a	*'P. mnaidriensis'*	All (East Sector)	96.5	±6.4	165.0	±10.1
SR5b	*'P. mnaidriensis'*	All (East Sector)	102.6	±6.4	180.2	±10.8
SR5c	*'P. mnaidriensis'*	All (East Sector)	89.7	±6.6	160.2	±11.4
SR5d	*'P. mnaidriensis'*	All (East Sector)	99.2	±8.5	175.7	±14.8
All (East Sector) mean			**93.5**		**165.7**	
SR1a	*H. pentlandi*	All (West Sector)	66.9	±3.9	115.9	±6.3
SR1b	*H. pentlandi*	All (West Sector)	68.2	±4.1	117.6	±6.6
SR6a	*H. pentlandi*	All (West Sector)	87.9	±6.9	155.9	±12.0
SR6b	*H. pentlandi*	All (West Sector)	90.6	±6.9	161.6	±11.9
All (West Sector) mean			**78.4**		**137.8**	
CONTRADA FUSCO MEAN			**88.2**	**±19.5**	**146.8**	**±28.7**

Table 3.6. ESR ages for Contrada Fusco, Sicily, arranged in rough stratigraphic order. Data from Rhodes (1996). Mean ages for L2, C4 and All (East Sector) order themselves in line with stratigraphy. True age is between EU and LU ages, with LU age more usually closer to true age (Grün 1989). EU is early, and LU is late model of uranium uptake.

Site	Species	Additional Notes	ESR Age (ka)		AAR Age (ka)	
Katharo Basin I	*Hippopotamus*	suggest order of magnitude only	846.0	±170	320	±64
Katharo Basin III	*Hippopotamus*	suggest order of magnitude only	512.0	±102	625	±125
Katharo Basin IV	*Hippopotamus*	suggest order of magnitude only	475.6	±95	469	±94

Table 3.7. ESR ages for Katharo Basin, Crete. AAR ages are provided for comparison. Reese *et al* (1996) note that these ESR ages should only be used to suggest the order of magnitude. Uranium uptake model and annual dose measures are not stated. ESR and AAR ages are of the same order of magnitude. Relative age of sites are not consistent between methods.

Site	Species	ESR Age (ka)		AAR Age (ka)	
Asproyi	*Phanourios*	639.5	±128	-	-
Vokolosspilios	*Phanourios*?	10.9	±2	13	±3
Pervolia	*Phanourios*	8.5	±2	8.0	±2
Dragontovounari	*Phanourios*	6.8	±1	9.0	±2
Mandres Virilas	*Phanourios*	10.0	±2	8.0	±2
Arkhangelos	*Phanourios*?	7.5	±2	11.5	±2
Ayios Phanentos	Phanourios	18.3	±4	-	-

Table 3.8. ESR ages for Cypriot localities, with AAR ages for comparison. Uranium uptake model and annual dose measures are not stated. AAR and ESR dates are in broad agreement for *Phanourios* sites in Cyprus, and are also comparable to ^{14}C and AAR dates from Akr. Aetokremnos, where the presence of *P. cypriotes* has been positively identified. This provides independent support for the age of Akr. Aetokremnos and the validity of Cypriot AAR dates calibrated to that site.

3.3.4. U-series dating

U-series dating is a radiometric technique based on the complex decay series of uranium (^{238}U and ^{235}U) and thorium (^{232}Th) isotopes, which each have a half-life of ~ 700 ka, but decay to intermediary nuclides with widely different half-lives (Walker 2005, Bourdon *et al* 2003). Uranium and thorium isotopes are naturally occurring, but uranium is soluble while thorium is not. Thus ^{238}U and ^{235}U present in the water are secreted (following uptake during life) or precipitated in carbonate materials such as shells, bone, spelothems and travertines, and then begin to decay; the daughter products can then be measured to provide an estimate of age since deposition/secretion, as being insoluble they would not be present in the initial carbonate structure (Walker 2005). In closed-system environments (i.e. where all uranium isotopes and their decay products are authigenic, and are not affected by subsequent uptake or leaching of uranium), ^{230}Th/^{234}U dating provides a high-precision, robust chronological tool up to approximately 500 ka (Richards & Dorale 2003). Speleothem features of caves behave as a closed system, whereas bone does not. U-series dates on bone material are only considered reliable if a suitable diffusion-absorption model of post-depositional uranium uptake is included in the analysis (Walker 2005, Pike *et al* 2005). Such models were not widely adopted until the late 1990's (Millard & Hedges 1996), and earlier U-series dates on bone should be treated with caution.

A flowstone layer in San Teodoro Cave, Sicily, was dated to 32 ± 4 ka using ^{230}Th/^{234}U activity ratios, providing a maximum age for the dwarf elephant fossils overlying it (Bonfiglio *et al* 2008). This date can be considered reliable: flowstone is a closed-system, the dating method is well established, and the stratigraphical control at the site is good. U-series dates published for Charkadio Cave (Table 3.10) are all derived from bone samples, and are not corrected for post-depositional uranium uptake (Bachmayer *et al* 1984). Independently published uranium levels for elephant remains from Charkadio Cave vary from 0.83-4.00 parts per million (ppm); significantly lower than those from other Pleistocene sites in Crete and mainland Greece (Theodorou *et al* 1985-6). Whether these low levels are indicative of a low level of uranium uptake, or a high level of leaching has not been established, providing no additional confidence in these dates. The variation between samples could be due to differential uptake conditions within the site/between different materials (e.g. bone vs tusk), or to the differing antiquity of each sample. Volcanic tuff has been used to infer and validate the age of deer material at Charkadio Cave (3.4.4) but cannot, at present, validate the U-series dates from Tilos. Given the acknowledged limitations of this technique on bone, these dates must be treated with caution (Table 3.10).

3.4. Island-wide geochronological correlation

Correlating the chronological occurrence of dwarf elephants within and between islands draws on both relative and absolute dating information, and on biostratigraphical theories. The first two lines of evidence have been covered in some detail above and in Appendix 1, outlining what is known about the

Locality	Species	Reference	Dose rate measured?	Uranium concentration	EU & LU estimates?	Reliability
Sicily						
Contrada Fusco	*'P. mnaidriensis' H. pentlandi*	Rhodes (1996)	Yes	variable between teeth, site mean more reliable	EU: 88.2 ±19.5 LU: 146.8 ±28.7	**HIGH**
Crete						
Katharo Basin	*Hippopotamus*	Reese *et al* (1996)	Unknown	Unknown	No model specified	**LOW**
Cyprus						
All	*Phanourios*	Reese 1995	Unknown	Unknown	No model specified	**LOW**

Table 3.9. Reliability of published ESR dates. ESR dates for Contrada Fuscon, Sicily, are accompanied by the relevant dose and uranium uptake information to assess reliability. Uranium uptake is variable between samples, indicating that a mean age of all samples is more appropriate. LU and EU models indicate the potential age range, and thus the precision of the age estimate. ESR dates for Cyprus and Crete are published without any of the requisite information, and must be treated with caution.

Locality	Sample	Reference	Stratigraphic association	ka	Closed system?	U-uptake corrected?	Reliability
Sicily							
San Teodoro Cave	flowstone	Bonfiglio *et al*. 2008	underlies *'P. mnaidriensis'*	32 ± 4	Yes	N/A	HIGH
Tilos							
Charkadio Cave	elephant bone?	Bachmayer *et al* 1984	direct: *P. tiliensis*	21.5 ± 1.7	No	No	LOW
	elephant bone?	Bachmayer *et al* 1984	direct: *P. tiliensis*	31 ± 1.7	No	No	LOW
	deer bone?	Bachmayer *et al* 1984	underlies *P. tiliensis*	140 ± 11	No	No	LOW

Table 3.10. Reliability of U-series dates from dwarf elephant localities. See text for discussion

stratigraphic provenance of material, and the reliability of the absolute dating information. Beyond being identified as Pleistocene deposits, the stratigraphy of karstic in-fills cannot be directly compared and correlated between sites, even within an island. Published dates have been shown to (i) have low reliability/precision in most instances, and (ii) date specimens whose exact provenance or stratigraphical relationship with dwarf elephant material is questionable. Consequently, the overriding tool used to temporally correlate deposits is biostratigraphy.

Simplistically, biostratigraphic schemes group sites or stratigraphic layers on the basis of shared taxa. They are, therefore, only as good as the taxonomic framework they are built upon. Given the taxonomic revision necessary for dwarf elephants (Chapter 4), it is likely that other taxa merit similar investigation, undermining confidence in the power and robustness of biostratigraphical (and biogeographical) correlations. Species presence/absence data is used in support of both biogeographical and biostratigraphical arguments, rendering them non-independent, although this has not prevented palaeobiogeographical patterns from being inferred (Marra 2005). There is also potential for circularity in using biostratigraphy to identify coeval taxa, and ultimately biostratigraphic groupings of taxa are themselves hypotheses of contemporaneity to be tested. The lack of robust absolute or relative dating information for the Mediterranean islands prevents a direct test of Mediterranean biostratigraphical schemes, and thus a broader discussion of the mutual support between biostratigraphy, stratigraphy and absolute dating is necessary to reconstruct dwarf elephant temporal distributions.

3.4.1. Malta and Sicily

The taxonomy of the faunas of Sicily and Malta are closely linked. Since Spratt (1867) postulated a land-bridge connection between the two islands, conspecificity of taxa has been assumed without recourse to detailed taxonomic verification. Consequently, the biostratigraphies of these islands are also linked and must be discussed together, although as with biogeographical reasoning this may be inappropriate (section 3.2). The majority of work on biostratigraphical correlation and the erection of faunal complexes has been based on Sicilian sites (e.g. Bonfiglio *et al* 2002, and references therein). Maltese taxa have only loosely been incorporated into these schemes (Hunt & Schembri 1999), and contemporaneity is generally assumed alongside conspecificity.

Three faunal complexes (FC) are recognized for the dwarf elephant chronology of Sicily. From oldest to youngest these are: the '*E. falconeri* FC', the '*E. mnaidriensis* FC' and the San Teodoro-Pianetta FC (Bonfiglio *et al* 2002, Bonfiglio *et al* 2008, Masini *et al* 2008). Each faunal complex is characterized by a suite of species, of which the mammals are best known (Table 3.11). For each of these faunal complexes, there are unique, or 'diagnostic', taxa that are key to biostratigraphical delineation: *P. falconeri* and, possibly, *L. cartei* for '*E. falconeri* FC'; *Panthera leo spelaea* and *H. pentlandi* for '*E.*

mnaidriensis FC'; and *Equus hydruntinus*, *Erinaceus europaeus*, *Microtus savii*, *Apodemus* cf. *sylvaticus* and *Crocidura* cf. *sicula* for San Teodoro-Pianetta FC (Marra 2005, Masini *et al* 2008).

A full assessment of Sicilian faunal complexes is beyond the scope of this thesis. However, a number of problems can be identified. First, with the exception of the San Teodoro-Pianetta FC, no Middle Pleistocene Sicilian faunal complex is represented by a 'type assemblage' (a well defined, single stratum containing all members of the FC, in clear stratigraphical association). Instead, the faunal lists for the '*E. falconeri* FC' and '*E. mnaidriensis* FC' appear to have been constructed through the partial correlation of faunal associations, as linked by the presence of diagnostic taxa, and are thus at risk of false correlations across time-averaged assemblages. Second, the taxonomic validity/integrity of these diagnostic taxa may be questionable, particularly as the parallel evolution of traits is seen in insular taxa (Chapters 4 & 6). Third, published biostratigraphical correlations and discussions of faunal turnover do not fully account for taxonomic revision/synonymy, suggesting a lack of taxonomic rigour in their construction. For example, *C. sicula*, the extant Sicilian/Gozo shrew diagnostic for the faunal turnover between the '*E. mnaidriensis* FC' and the San Teodoro-Pianetta FC (Masini *et al* 2008), is considered synonymous with *C. esuae*, a shrew present in both the '*E. falconeri* FC' and the '*E. mnaidriensis* FC' (Dubey *et al* 2008). Fourth, the small number of diagnostic taxa for each faunal complex means that FC attribution is susceptible to taphonomic bias: many sites/strata may not be positively identified. Finally, clear stratigraphical association between faunal complexes is not evidenced, to the best of my knowledge: thus the relative age of these FC, and thus their constituent taxa, has not been fully verified except by disputed dating methodologies (see below for further discussions). With these issues in mind, I have returned to first principles regarding the faunal correlations of Sicilian and Maltese dwarf elephant localities, and discuss them on the basis of their shared fauna rather than through the additional interpretive filter of faunal complex assignation.

Faunal correlations of Maltese and Sicilian dwarf elephant localities

There are no published absolute dates for Maltese elephant localities, making direct temporal correlation with Sicilian localities impossible. Biostratigraphical correlations between dwarf elephant localities on Sicily and Malta can be directly established from the published faunal lists for those sites (Table 3.11; data collated from Appendix 1). As already mentioned, the synonymy of Maltese and Sicilian endemics has not been independently verified, and thus published faunal lists must be treated with caution; for this exercise I assume taxonomic attributions are correct, and this would be expected to increase the chances of faunal correlation between Sicilian and Malta localities (and thus increase the risk of Type II error). In addition, I treat published references to '*P. melitensis'* and *P. falconeri* independently, despite probable synonymy (Chapter 6), to establish if there is any biostratigraphical separation of these taxa that might support species delineation (none occurs on Malta; the stratigraphical separation of different-sized elephants at Luparello Cave does not influence the synonymy of these taxa; Chapter 6). Maltese sites do not conform to established Sicilian faunal complexes, even allowing for

	E. falconeri FC [F]	*E. mnaidriensis* FC [M]	San Teodoro-Pianetta [S]	**Spinagallo Cave,** Layer 4	**Spinagallo Cave,** Layer 3	**Luperello Cave**	**Puntali Cave,** Brugal 1987, Layer 3	**Puntali Cave,** Brugal 1987, Layer 2	**Za Minica Deposit**	**Za Minica,** Layer 4	**Za Minica,** Layer 2	**San Teodoro Deposit**	**San Teodoro Cave,** Burgio & Di Patti, Layer 2	**San Teodoro Cave,** Bonfiglio *et al* 2008, Unit B	**Zebbug Cave**	**Maidra Gap**	**Benghisa Gap**	**Gandia Fissure**	**Ghar Dalam,** *Hippopotamus* layer	**Ghar Dalam,** *Cervus* Stage	**Ghar Dalam,** Carnivora Stage
Small Mammals																					
Maltamys sp.																			X		
Crocidura esuae				?	?														?	?	?
Leithia melitensis				X		X									X	X	?	X			
Leithia cartei	?			X		X									X		?		X		
Erinaceus europaeus														X							
Microtus (Terricola) savii														X							
Crocidura cf. sicula *														X					?	?	?
Apodemus cf. sylvaticus														X							
Large Mammals																					
Vulpes sp.	?					X															
Ursus sp.	?					X															
Palaeoloxodon falconeri				X		X							?		X	?	?		?		
Lutra trinacriae																					
Panthera leo spelaea																					
Hippopotamus pentlandi					X		X		X				X					?	?		?
Palaeoloxodon mnaidriensis					X		X	X		X			X	X	?	X	X	X	?		?
Crocuta crocuta spelaea								?		X			X	X							
Cervus elaphus siciliae								X		?	X		X	X							
Dama carburangelensis														X							
Bison priscus siciliae														X							
Bos primigenius siciliae								X		X				X							
Ursus arctos														X							X
Canis lupus								X		X				X							X
Vulpes vulpes														X							X
Sus scrofa								X		X				X							
Equus hydruntinus								?						X							
Birds																					
Cygnus falconeri															X	X	X	X			
Non-FC taxa																					
Palaeoloxodon melitensis						X									X	X	X		?		?
Hippopotomas melitensis																		?	?		?
Hippopotamus minor																		?	?		?
Bos sp.								X												X	
Cervus elaphus																				X	X
Pitymys melitensis																				X	X
Faunal Complex				**F**	**M**	**F**	**M**	**M/S**	**M**	**M/S**	**M/S**	**M**	**M/S?**	**S**	**-**	**-**	**-**	**M**	**M?**	**M/S?**	**M/S?**

Table 3.11. Faunal association of Sicilian and Maltese sites. Key mammalian and bird taxa for each Sicilian faunal complex (FC) relevant to dwarf elephant chronology are listed. Presence in each FC is shown by grey shading (after Masini *et al* 2008). Underlined taxa are considered 'diagnostic'. Identifiable stratigraphic layers are treated independently for each site. **X** denotes published records of taxon in that layer. **?** denotes uncertain presence/inclusion in FC. Based on these fauna, each layer is assigned to a FC: **F** is '*E. falconeri* FC'; **M** is '*E. mnaidriensis* FC'; **S** is San Teodoro-Pianetti FC. Sites to the left of the dashed line are on Sicily, to the right, Malta. Data collated from references in site descriptions (Appendix 1).

potentially erroneous correlations due to incorrect 'lumping' of Sicilian and Maltese taxa, and for the synonymy of *P. falconeri* and '*P. melitensis'* (Table 3.11).

The three most taxonomically important Maltese dwarf elephant localities, Zebbug Cave, Mnaidra Gap and Benghisa Gap, cannot be assigned to any Sicilian faunal complex due to the association of *P. falconeri* and/or *'P. melitensis'* with *P. mnaidriensis* and *C. falconeri* (the endemic, giant swan) (Table 3.11). While stratigraphic information from Zebbug Cave and Benghisa Gap is inconclusive as to the stratigraphical association of these taxa, Adams' records for Mnaidra Gap repeatedly state their co-occurrence in otherwise well-stratified layers (Appendix A1.1.2). This calls into question the validity of Sicilian faunal complexes for Malta. In addition, with the exception of Ghar Dalam, and possibly Gandia Fissure, there is a lack of association between *Hippopotamus* and *P. mnaidriensis* which is consistently seen at many Sicilian localities (Table 3.11). This raises additional questions about the biostratigraphic and biogeographic correlations within Malta (e.g. are Ghar Dalam '*P. mnaidriensis'* contemporaneous with and/or conspecific to Mnaidra Gap *P. mnaidriensis*?). An unpublished ESR date of 115 ± 10 ka exists for a *Hippopotamus* molar from Ghar Dalam (Bouchez *et al*, cited in Hunt & Schembri 1999) which, while its reliability cannot be assessed, is in-line with ESR ages for Sicilian *Hippopotamus.* The associated fauna in the hippo layer at Ghar Dalam is also consistent with the *'E. mnaidriensis* FC' (except for the presence of *L. cartei* which is only tentatively incorporated into Sicilian faunal schemes), suggesting Ghar Dalam and Sicilian '*P. mnaidriensis'* may be biostratigraphically correlated with each other but not to other Maltese *P. mnaidriensis*. Given the phenetic groupings of Maltese and Sicilian dwarf elephants (Chapter 6), this may well indicate a more complex picture of dwarf elephant evolution than previously envisaged.

The lack of congruence between Sicilian and Maltese faunal assemblages could reflect the lack of research on Maltese material (as evidenced by the multiple elephant and hippo taxa listed for Ghar Dalam), or the possibility that fossil assemblages at Zebbug Cave, Mnaidra Gap and Benghisa Gap are time averaged. The faunas of Malta and Sicily are also obviously related. Nevertheless, the data in Table 3.11 clearly show that Sicilian-Maltese faunal correlations are not simple (*contra* e.g. Hunt & Schembri 1999, Marra 2005).

Biogeographic (and, by extension, biostratigraphic) associations between Malta and Sicily are expected based on their close geographic proximity: Sicily acts as a filtering barrier between Malta and mainland Italy. However, as shown earlier, the geographic evidence for a contiguous Sicilian-Maltese insular environment at sea-level low-stands is not sufficient without the added reasoning of biogeographic correlations. Population vicariance as a result of sea-level rise can be expected to occur between Maltese and Sicilian taxa, as well as with mainland taxa, and the independent evolution of endemism is likely. Given the multiple interglacial – glacial cycles of the Quaternary, repeated vicariance, and thus taxonomic divergence, is also to be expected. Previous biogeographic and biostratigraphic analyses do not allow for this scenario, with circular assumptions of 'conspecifity' equalling contemporaneity hampering research into the evolution of endemism.

Based on the current evidence, it is not possible or appropriate to assign Maltese elephant localities to Sicilian faunal complexes: more work on the synonymy and interrelationships between Maltese and Sicilian taxa must be completed, in addition to the work on dwarf elephants in this thesis. Reliable dates are also needed for independent verification of contemporaneity of taxa/strata/sites within and between islands. Only then will a full picture of Malta and Sicily's biogeographical and biostratigraphical relationships be possible, offering great potential for understanding the evolution of the islands' faunas. This thesis offers the first step towards this by assessing the inter-relationships of Sicilian and Maltese elephants.

Temporal distribution of Maltese elephants

Given the lack of stratigraphical and dating evidence for Malta, and that it is inappropriate to apply Sicilian biostratigraphic schemes to Maltese elephants, there are no good data for the temporal distribution (relative or absolute) of Maltese elephants. Only Ghar Dalam and Mnaidra Gap have published stratigraphical associations between multiple dwarf elephant taxa: systematic revision tests whether multiple taxa are present at these sites (Chapter 6). For other localities, all dwarf elephant material must be treated as potentially contemporaneous/conspecific. Temporal distribution cannot inform evolutionary hypotheses on Malta.

Temporal distribution of Sicilian elephants

AAR dates for *P. falconeri* specimens from Spinagallo Cave and Luparello Cave, and on '*P. mnaidriensis'* (and *H. pentlandi*) from Puntali Cave have been attached to the '*E. falconeri* FC' and '*E. mnaidriensis* FC', respectively, based on these species presence in their eponymous faunal complex (note: my recalculated ages are younger by up to 100 ka (Table 3.5). However, biostratigraphic correlations for dwarf elephant taxa are imprecise and problematic (Table 3.11, Figure 3.6), and AAR dates should be treated with caution. No Sicilian horizons or samples were dated using more than one geochronological method, preventing a direct comparison between methods and a full assessment of the validity of the Sicilian AAR dates. The LU ESR dates for *H. pentlandi* and *P. 'mnaidriensis'* from Contrada Fusco are, however, similar to AAR dates for those taxa at Puntali and San Teodoro Caves, suggesting that the AAR approach may also be valid if biostratigraphical correlations are valid (although it must be borne in mind that LU dates represent the upper extreme of age estimate for these taxa, and thus the precision/accuracy of AAR dates is not verifiable). Two further pieces of evidence may lend weight to the AAR ages for Sicily. First, '*P. mnaidriensis'* and *H. pentlandi* material from Puntali Cave have similar AAR ages and these taxa are also stratigraphically associated at this site. Second, Puntali Cave material is thought to underlie a MIS 5e marine deposit (although this has not been verified), and the absolute age of 142 ± 36 ka for Puntali Cave '*P. mnaidriensis'* is consistent with this (Recalc. 1., Table 3.5). Despite this, it is clear that AAR dates for Sicilian material are problematic, not only in

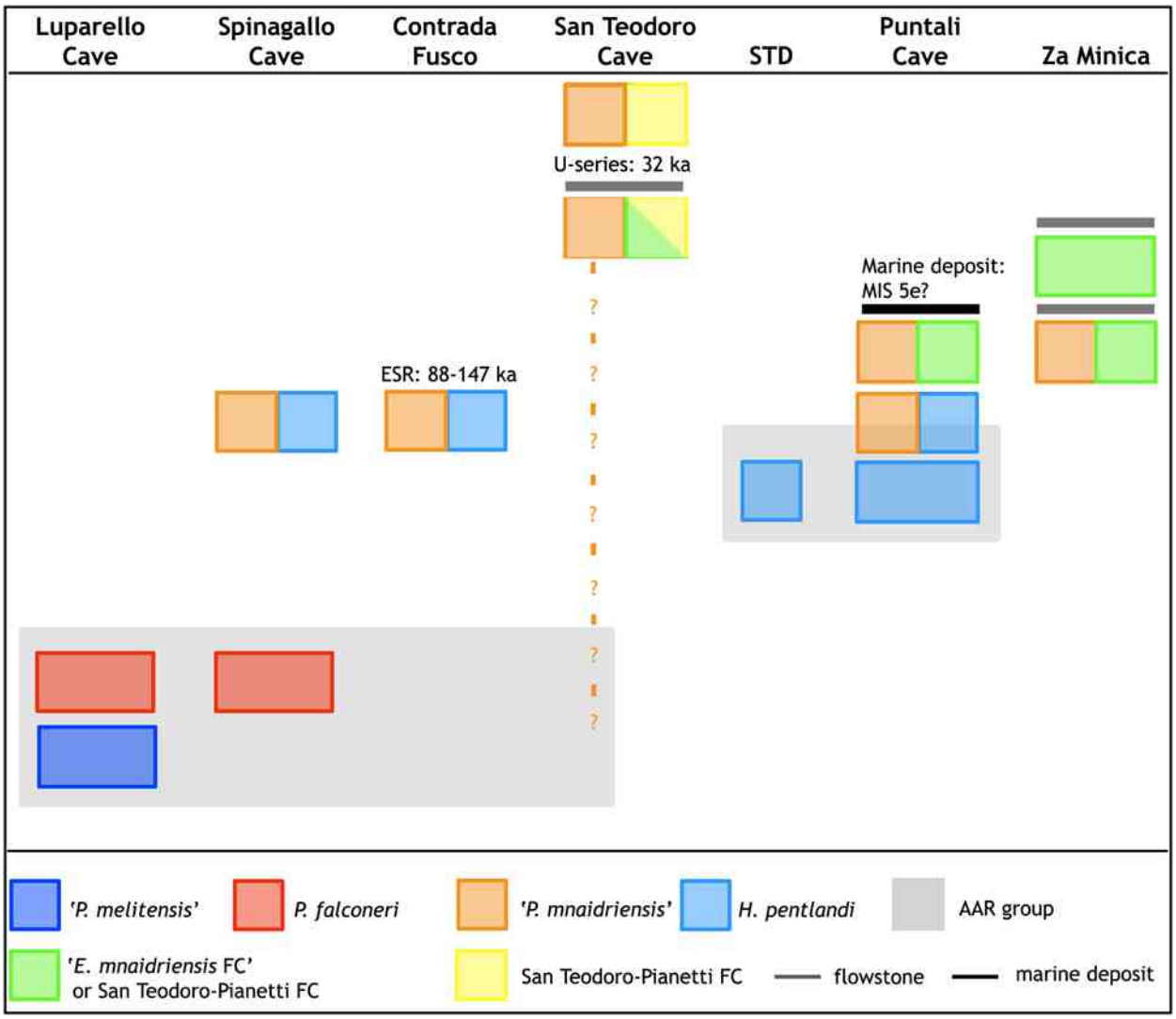

Figure 3.6. Summary of stratigraphical, biostratigraphical and dating evidence for the temporal distribution of Sicilian elephants. Each column is a different site, with stratigraphical layers ordered vertically from top to bottom and separated by a gap (i.e. top layer in figure is the top layer in the cave). Vertical 'axis' is not to scale, but provides a rough estimate of relative geochronology. Stratigraphical layers between sites are grouped horizontally by biostratigraphical association. Elephant taxa and *H. pentlandi* presence are shown individually, while the remaining taxa in that layer are grouped based on their consistency with published Sicilian faunal complexes (FCs). Reliable dating information is shown in black text. AAR dating is used to group material, but as it is considered unreliable and imprecise, absolute ages are not attached. As no evidence of *P. leo spelaea* is reported at the elephant localities under study, treating *H. pentlandi* separately means that the remaining mammal fauna for '*E. mnaidriensis* FC' is also consistent with San Teodoro-Pianetti FC. The verifiable presence of *E. hydruntinus* classifies the fauna as San Teodoro-Pianetti FC. Published provenance information for San Teodoro Cave is unclear as to the fauna underlying the flowstone layer, thus it is uncertain if the associated fauna should be ascribed to San Teodoro-Pianetti FC. **STD** is San Teodoro Deposit.

relation to the general methodology employed, but also in the internal story of Sicilian evolution that they represent (see below).

For *P. falconeri* localities Spinagallo Cave and Luparello Cave, the tension between the taxonomic revision of dwarf elephants and producing a biostratigraphic framework for dwarf elephant evolution is immediately apparent. The presence of *P. falconeri* is required for the attribution to '*E. falconeri* FC', thus biostratigraphic hypotheses of conspecifity and contemporaneity are identical, and one cannot be used as independent support for the other. For the remaining '*P. mnaidriensis'* localities, unless directly associated with *H. pentlandi* they cannot be definitively attributed to either '*E. mnaidriensis* FC' or San Teodoro-Pianetti FC. The only Sicilian locality with clear *H. pentlandi* association for which '*P. mnaidriensis'* material was available is Puntali Cave. However, the provenance of the elephant material is not recorded (Appendix A1.2.3), and so even here '*P. mnaidriensis'* material can not be unequivocally identified as belonging to a particular faunal complex. The reported co-occurrance of *P. falconeri* and '*P. mnaidriensis'* at San Teodoro Cave is also highly interesting on two counts: (i) similar co-occurrence in Maltese deposits and (ii) the old AAR dates for '*P. mnaidriensis'* enamel reported for this site. Unfortunately, only a limited amount of San Teodoro material was available for study, and I was unable to verify the occurence of *P. falconeri* at this site.

Sicilian AAR ages, relative or absolute, also suggest a more complex picture of than the one generally painted by faunal complex schemes. Published dates are used in support of an Early to Middle Pleistocene age for *P. falconeri* and a Middle to Late Pleistocene age for '*P. mnaidriensis'* (Palombo 2001, Bonfiglio *et al* 2002, Palombo and Ferretti 2005), and their eponymous faunal complexes. However, this generalization ignores the AAR age-grouping of '*P. mnaidriensis'* from San Teodoro Cave and Capo Peloro, as well as *P. antiquus*-sized taxa from Via Libertà, Palermo, in the older *P. falconeri* group (Bada *et al* 1991). AAR ages thus support the co-existence of *P. falconeri* and '*P. mnaidriensis'*, at odds with the current biostratigraphy. Alternatively, if these dates are treated as anomalous, then the reliability of the other AAR ages is called into question, even as a relative dating tool. Bada *et al* (1991) interpret the '*P. mnaidriensis'* and *P. antiquus* material that group with *P. falconeri* as a separate population from the later '*P. mnaidriensis'* group. If there are chronologically distinct populations of '*P. mnaidriensis'* on Sicily, that cannot be clearly delineated by morphology, this challenges the taxonomic validity of '*P. mnaidriensis'* and any biochronological inference based upon its presence.

ESR dates for *H. pentlandi* and '*P. mnaidriensis'* material from Contrada Fusco provide reliable evidence for the presence of these taxa on Sicily between MIS 4 and MIS 6 (Rhodes 1996). It is likely to be closer to the latter, as (i) LU models have been shown to be closer to independent age estimates and (ii) tooth enamel has been shown to underestimate true age (Grün 1989, Blackwell *et al* 1992). A pre-MIS 5 age would also be consistent with stratigraphic evidence and AAR dates for *H. pentlandi* and '*P. mnaidriensis'* from Puntali Cave. $^{230}Th/^{234}U$ dates from San Teodoro Cave indicate that '*P. mnaidriensis'* survived on Sicily until after 32 ± 4 ka, the same locality which yielded AAR dates of 370 ka for *P. 'mnaidriensis*' tooth enamel. Specimens referred to '*P. mnaidriensis'* need to be verified as true

conspecifics, and not just crudely grouped in a 'large-sized dwarf' dustbin taxon, and dating methodologies cross-validated before these data can be used to establish a temporal range for Sicilian '*P. mnaidriensis*'. However, based on the best available evidence, a 'large-sized' dwarf taxa appears to have been present on Sicily between 160 and 32 ka, and possibly earlier (Figure 3.6).

Belluomini & Bada (1985) used AAR dating to show that, on Sicily, *P. falconeri* was chronologically older than '*P. mnaidriensis'.* This overturned the previously held belief that *P. mnaidriensis* was the phyletic ancestor of *P. falconeri* (Pohlig 1891, Vaufrey 1929, Ambrosetti 1968). Although the validity of AAR dating has been questioned (section 3.3.2), stratigraphical evidence from Spinagallo Cave and Contrada Frategianni/Cozo del Re support the greater antiquity of *P. falconeri* than the larger-sized '*P. mnaidriensis'* and *H. pentlandi* from these sites, and thus their relative age is not dependent on the AAR dates alone. AAR dates suggest that the Spingallo Cave *P. falconeri* population is younger than that at Luparello Cavec (Table 3.5), however an error bar of ± 92 ka, combined with a lack of validation for this technique, ensures it can only be said that these populations cannot be separated chronologically. This is not the same as positive evidence for their being coeval. The apparent stratigraphical separation of *P. falconeri* and '*P. melitensis*' *sensu* Vaufrey (1929) at Luparello Cave is extremely interesting, presenting the only evidence of a medium-sized elephant on Sicily and suggesting it underlies the smaller *P. falconeri* (Appendix A1.2.2). It is tempting to speculate about the stratigraphical origin of the AAR dated Luparello Cave material, given the apparent greater antiquity of Luparello Cave elephants, and that Luparello Cave material is more generally lumped into a single taxon (Palombo & Ferretti 2005). Unfortunately there is no record of the provenance of the dated material (or for any of the excavated Luparello Cave material).

The lack of detailed provenance information for the Sicilian dwarf elephant material in this study prevents the use of temporal data to inform complex evolutionary hypotheses. In the absence of additional evidence for the antiquity of *P. falconeri*, the criticisms of the AAR methodology, and their inherent imprecision (a 20% error margin, Bada *et al* 1991), I take the recalculated dates as a guide only. Combining this with data for faunal associations inferred from non-elephant taxa, *P. falconeri* from Spinagallo and Luparello are e taken to be older than '*P. mnaidriensis'* from Puntali Cave, Za Minicam Contrada Fusco and at least some of the '*P. mnaidriensis'* from San Teodoro Cave (Figure 3.6). However, as the provenance of the San Tedodoro Cave material is unknown, the relative age of this material, and of the material of unknown provenance, is also unknown. This underlines the importance of 'bottom-up' taxonomy in Chapter 6.

3.4.2. Crete

Cretan *M. creticus* material or its sole locality, Cape Maleka (Appendix A1.3.1), have not been directly dated; however, *Hippopotamus* material from Katharo Basin, an upland basin of lacustrine deposits, 1120m above sea level, northeastern Crete, has been dated using a number of techniques. Based

on a combination of biostratigraphic argument and presumed body-size evolution trends, this material is believed to post-date the extinction of *M. creticus*, and is used to infer a minimum age of 800 ka for that taxon (Poulakakis *et al* 2002, Marra 2005, Poulakakis *et al* 2006).

Kritimys evolution and Cretan biostratigraphy

Mayhew (1977) hypothesized that the Cretan endemic rodent genus *Kritimys* represented a single phyletic lineage, increasing in size over time from *Kritimys kiridus* to *K. catreus*. However, this hypothesis was not corroborated by independent dating evidence: instead it reflected an assumption that body-size change would follow the island rule (see Chapter 1). Later researchers (e.g. de Vos 1984, Poulakakis et al 2002a, Marra 2005) have used Cretan murids as biostratigraphic markers, despite Mayhew's (1977) conclusion that their use for stratigraphic correlation was limited. In fact, *K. kiridus* is only definitely known from one, undated locality: Cape Maleka, also the sole (and type) locality of *M. creticus. K. catreus*, the hypothesised descendant of *K. kiridus,* is associated with *Hippopotamus* remains at Katharo Basin (de Vos 1984), but this material was not included in Mayhew's original analysis and validation of this taxon, and its 'position' within the evolving lineage is not verified. Indeed, Mayhew (1977) links *K. catreus* with deer localities, and appears to consider Cretan *Hippopotamus* and *M. creticus* contemporaneous. The taxonomy and evolution and temporal distribution of the *Kritimys* clade itself requires reassessment before it can be used as independent evidence for the relative age of *M. creticus.* Despite this, the biostratigraphical relationship between *M. creticus* and Katharo Basin continues to be widely accepted and cited (e.g. Mol *et al* 1996, Poulakakis *et al* 2002, Marra 2005, Poulakakis *et al* 2006).

Katharo Basin geochronology and the antiquity of M. creticus

A *Hippopotamus* bone from Katharo basin produced an uncalibrated ^{14}C date of 12,000 years (Bachmayer & Zapfe 1985). This ^{14}C date is an order of magnitude younger than the AAR dates published for the same site (see below), and was dismissed by later authors as 'wildly incorrect' on this basis (Reese *et al* 1996). Given the problematic nature of the AAR dates, however, incongruity of results between these methods cannot be used for mutual invalidation. Assessing the ^{14}C date on its own merits, a lack of published sampling and protocol detail returns a maximum confidence index (after Pettit, 2003) of 44%, indicating that – even with the most generous scoring criteria – this date should be treated with caution (Table 3.2). Dr. H. Zapfe indicated to Reese *et al* (1996, p.47) that it is 'possible that the sample had some deficiency'. It should be noted that this somewhat circumspect comment was made in response to the publication of the AAR dates, rather than an independent statement of problematic sampling. Ultra-filtration methods (which were not used for this sample) can push back the age of ^{14}C dates (Higham *et al* 2006); a reanalysed sample compared could conceivably fall within the error range of Katharo Basin AAR date calibrated to Akrotiri Aetokremnos (see below). However, ESR dates support an age for Katharo Basin in the same order of magnitude as AAR dates calibrated to Isernia La Pineta, Italy. While

ESR dates lack precision, the contemporary methodologies are still valid and reliable (section 3.3.3), and thus I favour them as an independent as an independent validator of the AAR dates, albeit only to an order of magnitude.

The published AAR ages for Katharo Basin range from 378 ±76 ka to 738 ±178 ka, with the greater age providing the 800 ka age cited for *M. creticus* (Marra 2005, Poulakakis *et al* 2006). My recalculation of these dates in line with the new age for Isernia La Pineta lowers this upper limit to 625 ±125 (Table 3.5, Recalc. Age 1). Thus, even if all the above criticisms of AAR dating and biostratigraphical inferences were unfounded, the 800 ka antiquity for *M. creticus* would still not be supported. This, in turn, undermines the temporal argument used for *Mammuthus* rather than *Palaeoloxodon* ancestry for *M. creticus* (Mol *et al* 1996, Poulakakis *et al* 2002, Poulakakis *et al* 2006; section 4.1.1), and reduces the purported antiquity of *M. creticus* aDNA (Poulakakis *et al* 2006).

The huge range of AAR ages for Katharo Basin (256 – 750 ka, Table 3.5) is difficult to interpret, as there is no detailed provenance information. Without this information, it is impossible to know whether (i) the *Hippopotamus* material was derived from the same horizon (and thus the variance in AAR dates reflects error in the dating methodology), or (ii) they derive from stratigraphically distinct deposits and the difference in AAR dates is representative of the first and last appearance dates for *Hippopotamus* at that site. If the former situation is true, then not only is the precision and usefulness of AAR dating of bone and tooth enamel further undermined (as it has been at other sites, e.g. Blackwell *et al* 1990), but – assuming some validity in the magnitude of the dates – the age of *M. creticus* could be substantially younger than even my recalculated age. It is important that authors who accept the validity of these dates use recalculated values, and also acknowledge the ambiguity present in the true age of these fossils. The use of an 800 ka date as a minimum age for *M. creticus* is therefore inappropriate.

3.4.3. Cyprus

There are no published dates associated with the *P. cypriotes* material from Imbohary (Appendix A1.4.1) included in this study. However, a number of other Cypriot sites have been dated using AAR, ESR and ^{14}C methods. These are biostratigraphically correlated with Imbohary through the presence of either *P. cypriotes* or *Phanourios* (the Cypriot dwarf hippopotamus). There is repeated association of *Phanourios* and *P. cypriotes* at Cypriot localities (although *Phanourios* material predominates: Reese 1995), supporting the co-occurrence of these taxa. An assessment of the available dating and stratigraphic evidence for these other sites allows an indirect estimate of the age of the Imbohary *P. cypriotes* material.

Only one dwarf elephant locality on Cyprus, Akrotiri (Akr.) Aetokremnos, has published ^{14}C dates (Reese 1995). None of these dates are directly sampled from *P. cypriotes* material. However, *P. cypriotes* material was recovered from Strata 2 and 4 (mostly from Strata 4b), and the interface between them, as well as on the surface of the deposit. The uncalibrated ^{14}C dates for shell, charcoal and *Phanourios* bone for each of these layers can be seen to be broadly in agreement with each other (Table

2.4.). Reese (1995, 1996) and Simmons (1989) make a clear case for the association of these faunal elements (and artefacts), with no evidence of reworking; reworked areas were identified at the front of the shelter, but undisturbed layers elsewhere supported association (Simmons 1989). The early (<9 ka) dates for the surface finds are considered to reflect post-depositional contamination, are disputed (Simmons 1989, Reese 1995), and thus I consider them to have very low reliability (Table 3.4).

Assessing the 27 published dates (Table 3.3), the maximum reliability scores achieved range from 41%-63%, indicating that all should be treated with caution. However, the high degree of internal correspondence in sample age within each stratum adds weight to the reliability of an average site age of 10 ka. Conversely, all strata appear to have the same age, lending little support for the site stratigraphy: Simmons (1989) clearly notes two distinct layers, separated by a sterile sand layer (he refers to these as Levels 1 and 2; cross-referencing his published dates with those of Reese 1995, Level 1 = stratum 2, Level 2 = stratum 4). Given that a hiatus long enough for a sterile sand layer to accumulate occurred between the deposition of Strata 4 and 2, this might have been reflected in the ^{14}C dates. Whether this casts doubt on the dates, the site's stratigraphic integrity, or reflects rapid deposition, cannot be demonstrated.

In arguing for the great antiquity of Akr. Aetokremnos, which could be the earliest evidence of human occupation on Cyprus, Reese (1996) cites AAR dates from there, and from other Cypriot localities, as additional support. It must be made clear that these AAR dates are not an independent line of evidence. On the contrary, they are calibrated to the 10 ka date for Akr. Aetokremnos. The range of alle/ile values (and therefore AAR dates) for Akr. Aetokremnos suggests that amino acid racemisation, as performed here, is at best an imprecise dating tool: *Phanourios* from Stratum 4b is reported as geochronologically younger than *Phanourios* from Stratum 2, when stratigraphical evidence predicts the opposite relationship (Table 3.5). Alternatively, as with the inconsistent ^{14}C dates, this could be evidence against the integrity of these strata, and may indicate reworking of deposits.

ESR dates of *Phanourios* from other Cypriot localities, however, provide independent support for an age in the order of 10ka rather than 100ka for the *Phanourios-P. cypriotes* fauna (Table 3.8), and corroborate the AAR and ^{14}C dates for Cyprus. However, as the ESR dates may lack precision, the accuracy of AAR and ^{14}C dates on Cyprus cannot be fully assessed. Fine-scale ageing of Cypriot deposits in general, and *P. cypriotes* specifically, seems inappropriate given the methodological constraints. Nevertheless, *P. cypriotes* appears to have an age in the order of 10ka, and Holocene survival cannot be ruled out. There is no available evidence for the maximum age of this taxon.

3.4.4. Tilos

Dwarf elephants excavated at Charkadio Cave (Appendix A1.5.1), are often described as the last surviving European elephants (e.g. Theodorou 1990, Palombo 2001a, Poulakakis *et al* 2002b). However, the published dates must be treated with caution (Tables 3.2, 3.4 & 3.10), and the cave stratigraphy has

been described piecemeal, resulting in ambiguity surrounding key features such as the co-occurrence of deer and elephants, and the nature and distribution of tuff deposits (Appendix A1.5.1). Uncalibrated ^{14}C and U-series dates exist for two different stratigraphic sections of the cave, for which no definitive cross-check between horizons is possible, beyond the presence of *P. tiliensis* in both. *P. tiliensis* bones directly dated to 4.4 ka and 7.1 ka were excavated from one section described as a cave loam mixed with tuff, containing dwarf elephant bones and human artefacts (Bachmayer & Symeonides 1975); however, recent taphonomical work challenges this association, and suggests that reworking of these deposits had occurred (Theodorou *et al* 2007). Bachmayer *et al* (1984) summarize the stratigraphy of the second section as follows:

Depth:	**Dated to:**	**Fauna/depositional features:**
0.6m	17 ka (^{14}C)	dwarf elephants
2.5m	21.5 ka(U-series)	↓
3.1m	30.6 ka (U-series)	↓
3.5-3.6m	35-45 ka (^{14}C)	calcite layer
4.8m to 6m	140 ka (U-series)	dwarf elephants & normal sized deer

The co-occurrence of deer and elephant beneath the calcite layer is clearly stated. Theodorou (1988), however, describes a different stratigraphy which has superseded that of Bachmayer *et al*. (Theodorou 1990, Poulakakis *et al* 2002b): dwarf elephant bones to a depth of 3.9m, followed by a sterile layer, then from 4.5 to 7m a layer containing only deer. No detailed discussion exists as to why the original stratigraphy was discredited. Deer remains are still cited as 140 ka, and dwarf elephant remains as 45 - 3.5 ka (Theodorou 1990, Theodorou *et al* 2006). This suggests dates were directly derived from bones of the respective taxa (sampling procedure is unclear in Bachmayer *et al* 1984), allowing the geochronology to be retained even if the stratigraphic association of deer and elephant was overturned. Published dates may be problematic (sections 3.3.1 & 3.3.4): the 35-45 ka date for the calcite layer is at the limits of ^{14}C dating, and can only be considered a minimum age, and recent attempts to date *P. tiliensis* material from Charkadio Cave at the Oxford Radiocarbon Accelerator Unit failed due to lack of collagen preservation (A. Lister, pers. comm.), casting further doubt on the preservation conditions of the cave. U-series dates are based on bone, which is not a closed system, and are thus also potentially erroneous (Table 3.10). The ^{14}C and U-series dates correctly order the samples according to horizon depth (Appendix A1.5.1), lending each other mutual support; however, without an undisputed date as arbiter, no indication of a well-defined internal stratigraphy for the *P. tiliensis* layer (Appendix A1.5.1), and no horizons dated by both methods for comparison, this cannot provide evidence for the accuracy of each date. Volcanic tuff evidence also cannot validate U-series dates without direct dating of the deposits in Charkadio Cave (section 3.2.2).

Consequently, a Holocene survival for *P. tiliensis* is not ruled out, but the maximum antiquity of this taxon, and the preceding deer layer, cannot be constrained using existing information. More dating

evidence is needed, and the presence of stalactite and tuff in the deposits appears to offer ample opportunity for this.

3.5. Implications for evolutionary hypotheses

In this chapter I made a careful audit of the palaeogeographical and geochronological evidence available for Mediterranean dwarf elephants, which highlights the lack of precision and reliability of absolute dating methods used for Mediterranean dwarf elephants. This prevents detailed, temporally-based evolutionary hypotheses from being tested and thus, at present, it is inappropriate to calculate evolutionary rates, or to assess the impact of time of isolation for these taxa. Similarly, given the cyclical nature of Quaternary climate, it is not possible to definitely establish the occurrence of dwarf elephants even to the level of MIS stage (and thus whether they are part of a warm- or cold-stage fauna). Palynological data provide no additional evidence, as few dwarf elephant localities have such information. As such, the interglacial nature of these endemic faunas is assumed, as these periods are expected to correlate with increased insularity due to sea-level rise, but cannot be verified. The palaeogeography of the islands is under-studied. Reconstructing past island areas (a key parameter in island biogeography) at eustatic high-stands is difficult and fraught with uncertainty, limiting the power and value of hypothesis-testing when investigating the impact of island area on degree of dwarfism. There is also evidence that Crete and Cyprus, and early Middle Pleistocene Sicily were isolated from the mainland during glacial periods and dwarf elephant evolution may have occurred over more than one glacial cycle.

Given the current low level of knowledge regarding the temporal distribution of dwarf elephants and even the most simple palaeogeographical reconstructions, I feel it is inappropriate to investigate adaptive trends and environmental and ecological correlates of dwarfism; for now, these must remain the province of interesting speculation. This thesis instead focuses on the parallel evolution of dwarfism, and its morphological, systematic and functional consequences. The findings of this chapter, and their impact on the evolutionary hypotheses to be tested in this thesis, are summarized below.

3.5.1. Western Mediterranean

1. Geographical, geomorphological and eustatic evidence does not support the existence of a contiguous Sicilian-Malta palaeo-island: **Maltese and Sicilian dwarf elephant taxa cannot be assumed to be conspecific on biogeographical grounds.**

2. There are no geochronological data to inform or constrain evolutionary hypotheses on Malta: **material from all sites must be treated as potential conspecifics, and delineated by morphology alone.**

3. South-east and Northern Sicily may have been separate islands in the early Middle Pleistocene: **Luparello Cave and Spinagallo Cave populations may have evolved independently, and may not be conspecific.**

4. Luparello Cave and Spinagallo Cave cannot be temporally delineated from each other, but this is based on (i) low-reliability dating and (ii) current dwarf elephant taxonomy: **material must be tested for conspecifity. Lack of conspecificity could challenge received wisdom of contemporaneity and/or or reflect geographical issues.**

5. Luparello Cave has two putative elephant species, separated stratigraphically: **the presence of multiple species at this site would be supported by geochronology.**

6. Luparello Cave and Spinagallo Cave elephants, on the one hand, are geologically older than those of Puntali Cave, Za Minica and San Teodoro Cave on the other: **The former are not descendents of the latter, and are temporally distinct. Temporal disjunction lends weight to species delineation between these two groups of sites.**

7. *'P. mnaidriensis'* material cannot be temporally sub-divided, due to a lack of detailed provenance information, combined with convoluted dating and stratigraphical evidence, despite biostratigraphic evidence that this taxon may occur over several different time periods, and may not be a single taxon: **the taxonomic integrity of *'P. mnaidriensis'* must be tested; however, a single species result may later be challenged by new geochronological data.**

8. The lack geochronological data on Malta, and the low precision/reliability of dating methods on Sicily, prevent absolute ages being assigned to Maltese and Sicilian elephant taxa: **taxa cannot be used to consider pan-Mediterranean temporal trends in insular evolution or time of isolation.**

3.5.2. Eastern Mediterranean

1. Geographical, geomorphological and eustatic evidence confirms the geographical isolation of Crete, Cyprus and Tilos: **this supports specific distinction for dwarf elephant taxa from these islands.**

2. A single taxon, from a single site, is sampled for each of Crete, Cyprus and Tilos: **taxonomic hypotheses are limited to testing the validity of these taxa.**

3. The antiquity and temporal distribution of *M. creticus* remains unverified: **this taxon cannot currently be used to consider pan-Mediterranean temporal trends in insular evolution or time of isolation.**

4. *P. cypriotes* and *P. tiliensis* material is likely to date to the order of 10 ka, and may have survived into the Holocene: **the antiquity of *P. cypriotes* and *P. tiliensis* are similar, and they may have evolved and/or gone extinct at similar times**

5. The maximum age of *P. cypriotes* and *P. tiliensis* cannot be assessed: **time of isolation cannot be estimated.**

Chapter 4: Systematics

4.1. Introduction

Any investigation into the evolutionalle be of insular dwarfism in Mediterranean elephants must be underpinned by a robust taxonomic framework. Without this, the number of dwarf elephant species is uncertain, and we cannot identify how many independent dwarfing events occurred within a genus, or – indeed – if dwarfing occurred across multiple genera. This chapter aims to provide such a framework. First, I summarize current and historical taxonomic usage (to identify hypothesized synonymy and conspecificity); second, I consider how best to recognize and delimit dwarf elephant species; third, I use these previous steps to inform my approach to systematic revision; finally, I analyze novel morphological data to produce a revised taxonomy for the Mediterranean dwarf elephants.

4.1.1. Dwarf elephant taxonomy and nomenclature

The existing taxonomy of Mediterranean dwarf elephants is convoluted, reflecting a mixture of nomenclatorial and palaeontological issues. Whilst nomenclatorial changes have, for the most part, followed authors' opinions as to the number, and con-specificity, of dwarf taxa, historical baggage remains in unresolved priority disputes and generic attribution. In this way, three levels of taxonomic confusion can be addressed: (i) the 'genera problem', (ii) the 'species problem' and (iii) the 'nomenclature problem'.

The genera problem

There are two disparate issues in the generic attribution of dwarf elephants: ancestry and nomenclature. For Sicily, Malta, Cyprus and Tilos, nomenclatorial issues predominate, reflecting the debate over the validity of the genus *Palaeoloxodon (Figures 4.1-4.3)*. *Elephas* was used synonymously with *Mammuthus* and *Palaeoloxodon* well into the 20th Century, and continues to be used for European *Palaeoloxodon* by many researchers to this day (e.g. Ambrosetti 1968, Bonfiglio *et al.* 2002, Palombo 2001a, Palombo 2007). However, *Palaeoloxodon* has been shown to be a monophyletic clade, including *P. antiquus*, *P. namadicus*, *P. naumanni* and the *P. recki* group (Davies 2002, Feretti 2007), and is accepted here as a valid genus (following Inuzuka & Takahashi 2003, Shoshani & Tassy 2005).

For Cretan taxa, putative ancestry has played a much larger role in recent taxonomic revisions (Figure 4.4). With the exception of Kuss (1965, 1966), who believed the African elephant genus *Loxodonta* should also be considered, the majority of authors have considered *Mammuthus* and

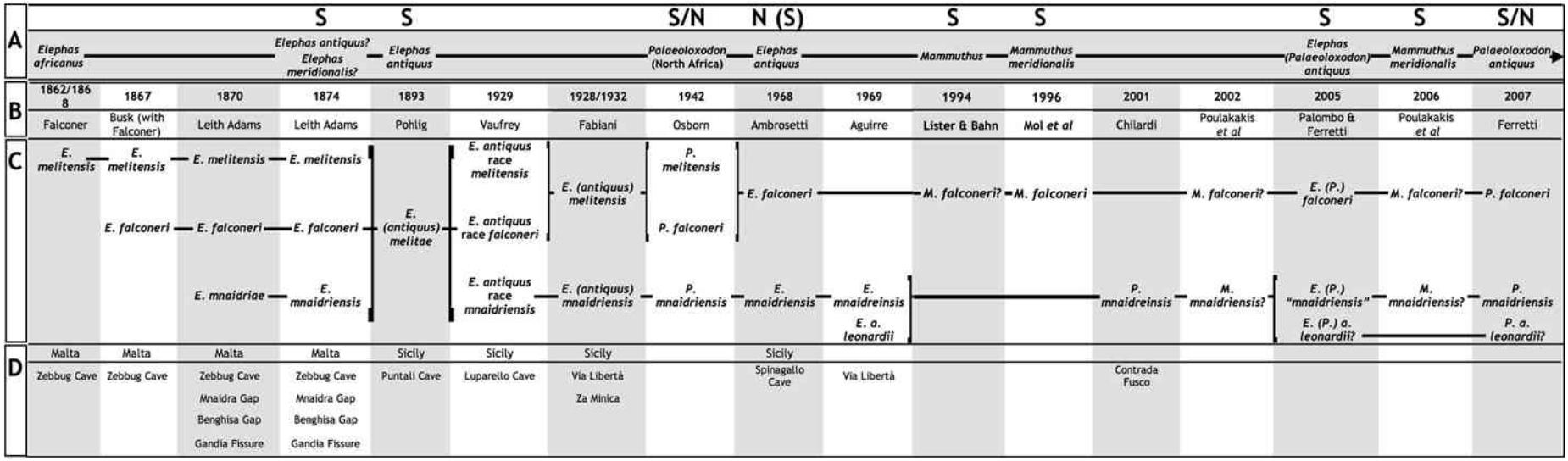

Figure 4.1. Systematic history of dwarf elephant taxa from Sicily and Malta. [A] Hypothesized mainland ancestor used for generic attribution of taxa. Before Osborn (1942) *Elephas* was widely used for all Elephantinae taxa. **S** denotes a change in genera/ancestral taxa based on systematic opinion, **N** denotes a nomenclatorial change. **N (S)** denotes a change that is primarily nomenclatorial, but has some systematic relevance: e.g. Ambrosetti considered *Palaeoloxodon* (*sensu* Osborn 1942) synonymous with *Elephas*, thus in part this was a nomenclatorial change, however he also clearly identified '*E'. antiquus* as the probable ancestor of dwarf taxa, which was never included by Osborn within *Palaeoloxodon*. Ferretti (2008; published on-line in 2007) verified both the validity of the genus *Palaeoloxodon* and inclusion of *P. antiquus* and *P. mnaidriensis* in that genus. This was a systematic change, accompanied by nomenclatorial change, that did not however alter Ferretti's previous position on ancestry. Ferretti did not directly address Mol *et al*'s (1996) or Poulakakis *et al*'s (2002, 2006) contention of *Mammuthus* ancestry. **[B]** Year and Author of publication. **[C]** Synonymy of dwarf elephant taxa: lines connect Linnaean binomials that refer to the same taxa. Brackets indicate lumping and splitting of taxa by different authors. **[D]** Locality of material used in new description of taxa or systematic revisions.

Palaeoloxodon as the likely progenitors of Cretan dwarf elephants (e.g. Mol *et al* 1996, Poulakakis *et al.* 2002a). These taxa are the only mainland genera present in Middle Pleistocene Europe and North Africa (Algerian *Loxodonta atlantica* specimens figured in Maglio (1973) show palaeoloxodontine characters, and suggest this taxon needs revision).

In practice, however, *P. antiquus* has been generally accepted as the ancestor to all Mediterranean dwarf taxa since Pohlig (1893) hypothesized the shared ancestry of Maltese and Sicilian dwarf taxa, synonymizing the three existing taxa (*'E. melitensis'*[1] Falconer 1867, *'E.' falconeri* Busk 1867 and *'E.' mnaidriensis* Adams 1874) to *'E. antiquus melitae'*. Prior to Pohlig (1893), debates occurred in tandem with wider discussion over the immutability – or otherwise – of species, ignited by Darwin (1859). As a consequence, discussion was more often concerned with similarity to known forms, rather than explicit hypotheses of descent or interrelatedness (indeed, Hugh Falconer, who described the first dwarf elephant taxon, *'E. melitensis'*, was not initially convinced by Darwin's theory, as can be followed through their correspondence (Appendix 4 and http://www.darwinproject.ac.uk).

Taxonomic affinity with *Palaeoloxodon* for Maltese, Sicilian, Cypriot and Tilos dwarf elephants, and for *P. antiquus creutzburgi* from Crete, has been established on morphological grounds, with these taxa exhibiting diagnostic *Palaeoloxodon* features (e.g. relatively narrow, high crowned molars; lozenge or 'cigar-shaped' enamel loops with medial expansions; distinctive early occlusal wear pattern, and – in Sicilian '*P. mnaidriensis'* – expanded parietal bosses and a well developed parietal-occipital crest, or frontal torus) (Bate 1905, Osborn 1942, Ambrosetti 1968, Theodorou 1983, Davies 2002, Poulakakis *et al.* 2002a, Palombo 2003; Ferretti 2008). Furthermore, ancient DNA (aDNA) evidence does not support a *Mammuthus* affinity for *'E.' tiliensis* (from Tilos) (Poulakakis *et al.* 2002b). However, as aDNA has yet to be extracted from a *P. antiquus* specimen, and Poulakakis *et al.* (2002b) instead showed *'E.' tiliensis* nested within extant and sub-fossil *Elephas*, this is only indirect evidence for *P. antiquus* ancestry.

Bate (1907) clearly documented the morphological similarity of *'E.' creticus* to *Mammuthus meridionalis*, noting in particular the low crowned nature of the teeth, but nevertheless assigned ancestry to *P. antiquus (Figure 4.4)*. This was in part due to a contemporary belief that *P. antiquus* was characterised by 'adaptability' and a propensity to dwarf on islands, but also to a lack of available information regarding the antiquity of the fossil record in Europe (Bate 1907). Bate had also found material referable to full-sized *P. antiquus* on Crete, and believed that it was not possible for the island to have maintained two contemporaneous species of elephant: thus with evidence of *P. antiquus* on the island, she reasoned it must be the ancestor of *'E.' creticus*. The attributed affinity of *'E.' creticus* to *P. antiquus* was therefore circumstantial.

[1] To enable the nomenclatural history to be followed in the text, I use each author's taxonomic usage, and place quotes around species or genus names that are at odds with my revised taxonomy.

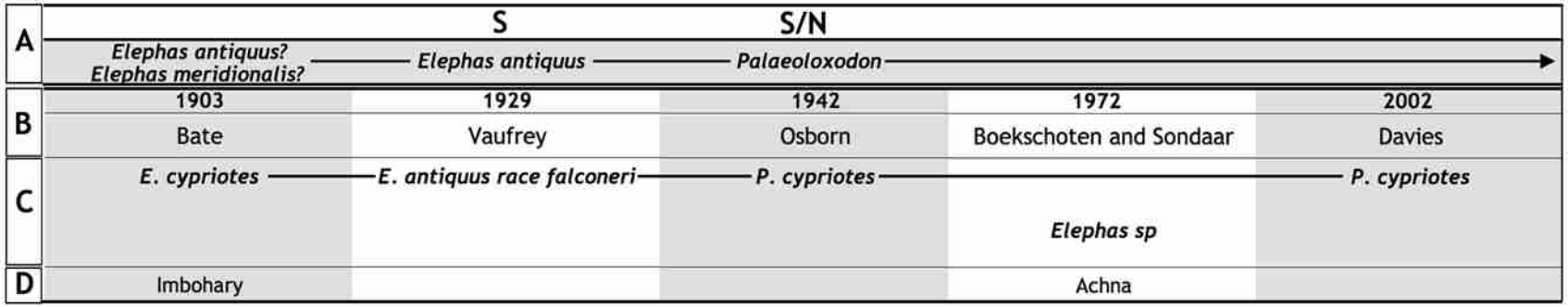

Figure 4.2. Systematic history of dwarf elephant taxa from Cyprus. [A] Hypothesized mainland ancestor used for generic attribution of *P. cypriotes*. Before Osborn (1942) *Elephas* was widely used for all Elephantinae taxa. **S** denotes a change in genera/ancestral taxa based on systematic opinion, **N** denotes a nomenclatorial change. **[B]** Year and Author of publication. **[C]** Synonymy of dwarf elephant taxa: lines connect Linnaean binomials that refer to the same taxa. **[D]** Locality of material used in new description of taxa or systematic revisions.

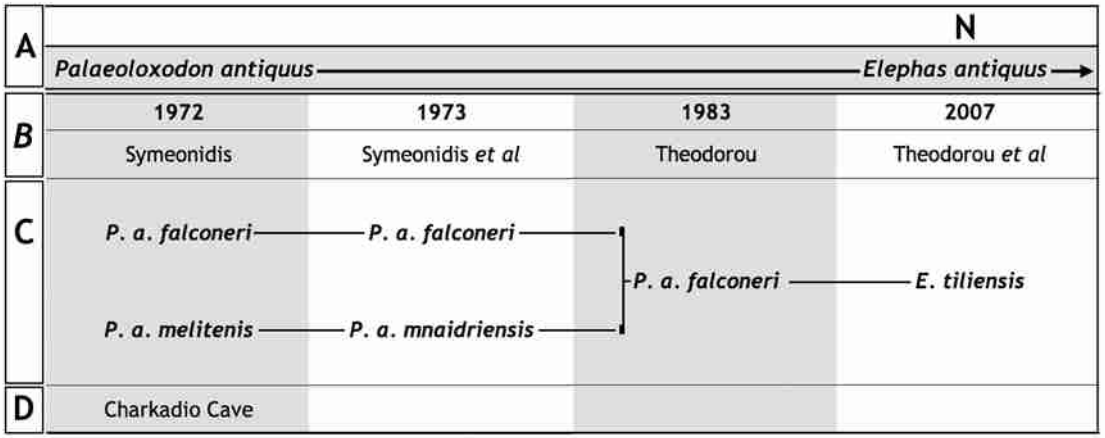

Figure 4.3. Systematic history of dwarf elephant taxa from Tilos. [A] Hypothesized mainland ancestor used for generic attribution of taxa. **S** denotes a change in genera/ancestral taxa based on systematic opinion, **N** denotes a nomenclatorial change. **[B]** Year and Author of publication. **[C]** Synonymy of dwarf elephant taxa: lines connect Linnaean binomials that refer to the same taxa. Brackets indicate lumping and splitting of taxa by different authors. **[D]** Locality of material used in new description of taxa or systematic revisions.

Recently, there has been a resurgence of interest in the possibility of a *Mammuthus* ancestry for some dwarf elephants. Lister and Bahn (1994) posited a possible *Mammuthus* ancestry for Sicilian *'E.' falconeri*, based on skull morphology (Figure 4.1). This suggestion was later dismissed by the authors (and removed from the 2nd and 3rd editions of the same book: Lister & Bahn 2000, 2007), but was re-iterated by Mol *et al.* (1996), who also proposed *Mammuthus* ancestry for *'E.' creticus (Figure 4.4)*. Beyond referencing Bate's (1907) description, their reasoning was not based on morphological assessment. Instead, Mol *et al.* (1996) asserted that the ages of the dwarf taxa pre-dated the first appearance date of *P. antiquus* in Europe, thus precluding it as a potential ancestor for *'E.' creticus* and for *'E.' falconeri*. Poulakakis *et al.* (2002a, 2006) re-stated Mol *et al.'s* arguments in support of *Mammuthus* ancestry for *'E.' creticus* and *'E.' falconeri*. Such arguments are spurious, and are not sufficient to merit taxonomic revision, even without reference to the large errors and uncertainties surrounding the dating of dwarf taxa (particularly on Crete; see section 3.4.2). First appearance dates for *P. antiquus* have also been pushed back to the Brunhes/Matuyama boundary (ca.780 Ka) at Slivia, Italy (Lister 2004). Taken alongside the potential rapidity of island dwarfism (Lister 1989), this invalidates the argument that *P. antiquus* cannot be a potential ancestor for these dwarf taxa.

Poulakakis *et al.* (2006) reported aDNA evidence for a *Mammuthus*, rather than *Palaeoloxodon*, affinity for *'E.' creticus (Figure 4.4).* The credibility of this study was called in to question owing to 'serious theoretical and methodological flaws' (Binladen *et al.* 2007, p.56): (i) two of the three nucleotides identified by Poulakakis *et al.* as 'diagnostic' for *Mammuthus* lay within the original primer-binding site used to amplify the aDNA fragment (Binladen *et al.* 2007), (ii) all three 'diagnostic' sites were found within GenBank sequences of the African elephant *Loxodonta spp.*, and are not *Mammuthus* autapomorphies (Binladen *et al.* 2007, Orlando *et al.* 2007), and (iii) Poulakakis *et al.'s* phylogenetic analysis identified *Mammuthus* and *Loxodonta* as sister-taxa, at odds with the elephant phylogeny based on whole mitochondrial and nuclear genome data (in which *Elephas* and *Mammuthus* are sister-taxa; e.g. Krause *et al.* 2006; Rogaev *et al.* 2006; Capelli *et al.* 2006; Miller *et al.* 2008), suggesting their results would not be robust to the addition of more aDNA data (Orlando *et al.* 2007). The low likelihood of aDNA being recovered from 800 ka material preserved in warm environments also cast doubt on the legitimacy of the claim (Smith *et al.* 2003, Binladen *et al.* 2006).

Further criticisms of Poulakakis *et al.* (2006) can be made: (i) DNA was extracted from a non-diagnostic fragment of rib bone collected in the vicinity of the area that *'E.' creticus* was excavated (Bate 1907, Poulakakis *et al.* 2006), but not definitely referable to *'E.' creticus,* (ii) the great antiquity of the material was inferred from the putative biostratigraphical position of the original *'E.' creticus* material, relative to hippo material from a different locality, dated using a disputed AAR methodology (see section 3.4.2), and (iii) in responding to criticisms of the likelihood of DNA amplification from 800 ka material, Poulakakis *et al.* (2007) stated the material was from a cave, where temperatures are lower and more stable. If this is the case then the sampled material, only attributable to *'E'. creticus*

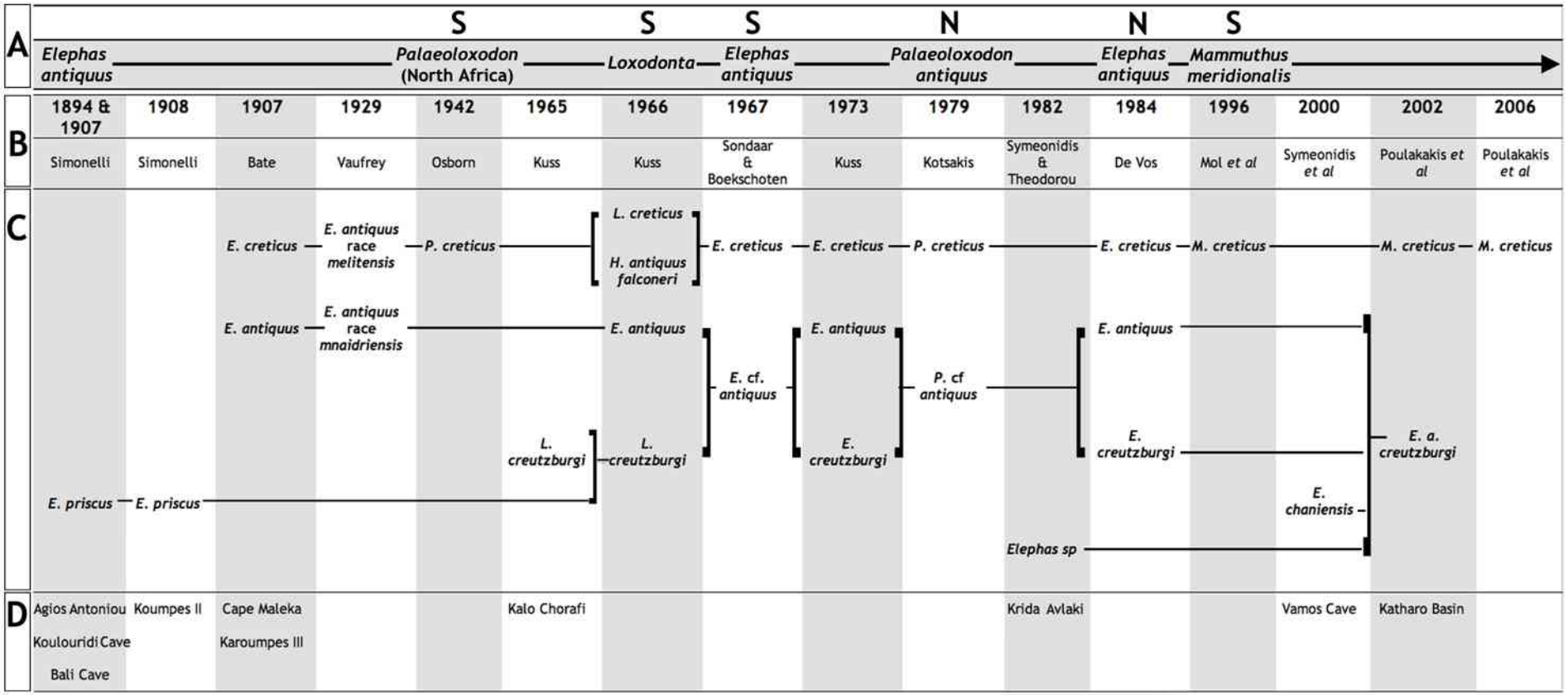

Figure 4.4. Systematic history of dwarf elephant taxa from Crete. [A] Hypothesized mainland ancestor used for generic attribution of *M. creticus*. Before Osborn (1942) *Elephas* was widely used for all Elephantinae taxa. **S** denotes a change in genera/ancestral taxa based on systematic opinion, **N** denotes a nomenclatorial change. **[B]** Year and Author of publication. **[C]** Synonymy of dwarf elephant taxa: lines connect Linnaean binomials that refer to the same taxon. Brackets indicate lumping and splitting of taxa by different authors. **[D]** Locality of material used in new description of taxa or systematic revisions

on the basis of its provenance, was not excavated from the type locality of *'E.' creticus*, which is now open coast line (Bate 1907; personal observation, Figure A1.9). In light of all these criticisms, Poulakakis *et al.*'s (2006) findings must be disregarded. The ancestry of *'E.' creticus* thus requires testing. There is no published evidence of any attempt to re-assess the morphological affinity of *'E.' creticus* since Bate's (1907) original description. There is also no reason to preclude the presence of dwarf mammoths in the Mediterranean, given the presence of *M. lamarmorae* on Sardinia, although the overwhelming presence of *Palaeoloxodon*-derived dwarfs is in itself interesting.

The species problem

The erection, description and subsequent synonymization of dwarf elephant species (Figures 4.1-4.4) has been closely tied to contemporary opinion on species concepts, geology and biogeography: all dwarf elephant species descriptions are post-Linnaean, post-"Origin of Species" but (with the exception of the Tilos elephants) pre-Modern Evolutionary (or 'New') Synthesis. The majority of dwarf taxa were first described in the late 19th and early 20th century: *'E. melitensis'* (Falconer, in Busk 1867), *'E'. falconeri* (Busk 1867) and *'E.' mnaidriensis* (Adams 1874), *'E.' cypriotes* (Bate 1904) and *'E.' creticus* (Bate 1907). All of these authors were therefore working within a recognizable Linnaean paradigm, with species description focused on diagnosis, but the influence of Darwin's *On the Origin of Species* became increasingly important (particularly in reference to later synonymy). With Darwinian debate focused on the role of variation in the origin of species, this naturally led to discussions regarding the temporal delimitation of species (a debate that is, as yet, unresolved).

Hugh Falconer, the first describer of a dwarf elephant, was a slow convert to the idea of the mutability of species. He saw in elephants an astounding lack of evidence for change through time (e.g. Falconer 1863; letter 3737, Appendix 4). His opinions on the nature of species tended towards 'lumping' rather than 'splitting', as demonstrated by his rebuttal of the ideas that Sumatran elephants constituted a different species to the Indian elephant (Falconer 1863), and he appears to favour continuity of characters within a population over the absolute amount of variation in the delineation of species (letter 2511, Appendix 4). It is therefore unsurprising that he described a single Maltese taxon from Zebbug Cave, '*E. melitensis*', with an estimated M3 plate count of 12 (Falconer, in Busk 1867), although he noted the presence of a second larger sized taxon (Busk 1867). Busk subsequently recognized three taxa of dwarf elephants in the Zebbug material (Figure 4.1), and described in detail the supposed differences between the two 'diminutive' forms, *'E.' melitensis* and *'E. falconeri'*. He suggested that the former species had a post-cranial morphology more similar to the African elephant, while the latter resembled the Asian, and that one 'probably exceeded the other in size' (Busk 1867, p. 230). Detailed comparative anatomy of the extant elephant postcrania has yet to identify clear-cut diagnostic characters for differentiating between these taxa. Adams (1874) later cast doubt on the presence of two small-sized taxa, but still referred some material to *'E. melitensis* (?*E. falconeri*)' and

thus did not explicitly synonymize these taxa. Adams (1874) confirmed the presence of a much larger Maltese elephant and named this *'E.' mnaidriensis*, with an M3 plate count of 12-13 (Adams 1874; Figure 4.1). Each of these authors brought to their arguments reasoning based on the amount of variation that can be accommodated in a species, and that species should be diagnosable based on these key characters.

Pohlig's (1893) synonymization and reclassification of these taxa to a sub-species of *P. antiquus* ('*E. (antiquus) Melitae'*; Figure 4.1) is evidence of the pervasive influence of Darwin (1859) and the ramifications it had on palaeontological taxonomy. Pohlig identified the dwarf elephants of Malta and Sicily as an small insular race of mainland European *P. antiquus*, recognizing the 'mutability' of species, but struggling with the idea of contemporaneous ancestral and descendent species, and with the delimitation of species boundaries within an anagenetic lineage. Pohlig (1893) also began the trend of synonymy between Sicilian and Maltese taxa that continues to this day.

Dorothea Bate's discovery of dwarf elephants on Cyprus (Bate 1904) and Crete (Bate 1907) expanded the biogeography of dwarf elephants. Until this point, dwarf taxa were known only from Sicily, Malta and Sardinia. Bate considered that these dwarfs represented a separate evolution of dwarfism on each island (Bate 1904, 1907; Figure 4.2 & 4.4), but relied on molar size- and shape-differences to justify her taxa, rather than emphasizing the evolutionary independence of these taxa. (This, and Vaufrey's subsequent synonymization of all dwarf taxa of equivalent size, regardless of island origin (Vaufrey 1929; Figures 4.1, 4.2 & 4.4), underline the lack of 'process' based species concepts in systematic research at that time. Even Osborn's subsequent re-erection of each insular taxon (Osborn 1942; Figures 4.1, 4.2 & 4.4) was based on his opinion on the validity of diagnosable characters (and in part reflected his general taxonomic exuberance on this front) rather than any arguments for phyletic independence between elephants from different islands.

In 1942, the same year as the posthumous publication of Osborn's *Proboscidea Volume II*, Julian Huxley's *Evolution: the Modern Synthesis* and Ernst Mayr's *Systematics and the Origin of Species* were published. This, and subsequent publications on the nature of species, brought about a key paradigm shift in systematics. Process was now explicitly linked to both the maintenance and evolution of species, with reproductive isolation, allopatric speciation and the biological species concept rapidly incorporated into contemporary biological opinion. From hereon, the discussion surrounding dwarf elephant systematics has recognized the significance of isolation on different islands in species delineation and the importance of dwarf elephants as 'natural experiments' in parallel evolution. The only exceptions to this are the Tilos dwarf elephants, attributed by Symeonidis to '*E. antiquus falconeri'* and either '*E. a. melitensis'* or '*E. a. mnaidriensis'*, on the basis of size (Symeonidis 1972, Symeonidis *et al.* 1973), following Vaufrey (1929) (Figure 4.3). This reasoning is unsupportable on biogeographical and biological grounds, but has only recently been rectified by the description of a single, sexually dimorphic species, *'E.' tiliensis* (Theodorou *et al.* 2007; Figure 4.3).

Within an island, however, debate regarding the number of species has continued. In Sicily and

Malta this has primarily related to discrimination between *'E. melitensis'* and *'E.' falconeri* (Figure 4.1), whilst on Crete the validity of *'E'. a. creutzburgi* as a distinct taxon from continental *P. antiquus* has generated the most interest (Figure 4.4). This latter reflects the perennial problem of distinguishing the – possibly arbitrary – point at which an evolving lineage becomes a new species. This study does not include sufficient large-sized Cretan fossils to address this issue.

The distinction between *'E.' falconeri* and *'E. melitensis'* on Malta was challenged within 10 years of their description (Adams, 1874). Researchers, however, have tended to follow Vaufrey (1929) and Osborn (1942) in attributing each taxon on Sicily and Malta to a different size class: *'E.' mnaidriensis* (considered a large-sized dwarf), *'E.' melitensis* (considered a medium-sized dwarf) and *'E. falconeri'* (considered the smallest dwarf taxon). The presence of a medium sized taxon remains controversial on Sicily, and thus *'E. melitensis'* has fallen out of use (Ambrosetti 1968, Caloi *et al.* 1996, Palombo & Ferretti 2005). The size difference between *'E.' mnaidriensis* and *'E.' falconeri'/ 'E. melitensis'* is apparent, but there was little emphasis on size difference between *'E.' melitensis* and *'E. falconeri'* in Busk's original description (Busk 1867). Adams (1874) goes on to state "there are intermediate-sized bones which easily bridge over the differences between the latter [*P. falconeri*] and the *Elephas melitensis*" (p. 118), which calls into question Vaufrey's and Osborn's later interpretation of these taxa. Nevertheless, this sized-based taxonomy has been very influential in Sicily, with small dwarfs (e.g. Spinagallo Cave specimens) attributed to *'E.' falconeri* and large dwarfs to *'E. mnaidriensis'* (Figure 4.1).

The presumed synonymy of Maltese and Sicilian dwarf elephants is based on geological and biogeographical argument, and has never been tested empirically (section 3.2.1). Fossil faunas also support a biogeographical link between these islands (Hunt & Schembri 1999). However, it must be borne in mind that conspecifity within any of these taxa, just as with the dwarf elephants, has in part been based on an *a priori* assumption of geographic contiguity and may not have been independently verified. Without additional geological data on the past surface area and contiguity of Malta and Sicily, the 'contextual' argument for synonymy of Maltese and Sicilian taxa should not be invoked, and requires testing using a systematic approach. However, given the potential problem of homoplasy in similar-sized dwarf (or giant, in the case of dormice and swans) taxa, systematic methods may not be able to fully resolve the problem.

The nomenclature problem

The use of *Elephas* is still widespread for all dwarf elephant taxa. In part this may reflect opinion on either the ancestry of the dwarf taxa, or the validity of the genus *Palaeoloxodon*, or both. For the most part, however, it results from a nomenclatorial inertia in research disciplines that incorporate, but are not concerned with the systematics of, Mediterranean dwarf elephant taxa (e.g. palaeoecology and biostratigraphy: Bonfiglio and Burgio 1992, Bonfiglio *et al.* 2002, Marra 2005; and meta-analyses of insular trends (the 'Island Rule'): Van Valen 1973, Heaney 1978, Millien *et al.*

2006, Raia & Meiri 2006).

Altering the usage pattern of *Elephas* rather that *Palaeoloxodon* in these disciplines will take time, but is necessary. *Palaeoloxodon* is widely accepted amongst elephant systematists, and the ongoing use of *Elephas* for *P. antiquus* and the Mediterranean dwarfs leads the uninitiated to assume that these taxa are more closely related to Asian elephants than they are to mammoths (currently these three genera form an unresolved trichotomy). In aDNA debates surrounding dwarf elephants, dwarf elephant DNA has been assessed for its affinity with *Elephas* versus *Mammuthus* because of the presumed systematic information contained in the generic attribution (‘*E.’ creticus* and *‘E.’ tiliensis*). There is no verified aDNA from *Palaeoloxodon* to test the dwarf elephant affinity or the relationships between *Mammuthus, Elephas* (*sensu stricto*) and *Palaeoloxodon*, and thus such comparisons are nonsensical. A change to the use of *Palaeoloxodon* would halt such confusion.

A second nomenclatorial issue in dwarf elephant systematics is that of priority and validity of *‘E. melitensis’* and *‘E.’ falconeri.* As noted above, *‘E.’ falconeri* is widely used to describe the smallest Sicilian and Maltese dwarf elephants. *‘E. melitensis’* has fallen out of use because it is thought to (i) describe a medium-sized taxon, whereas only two size classes of Sicilian dwarf elephant are widely recognized (the majority of 20th century dwarf elephant research has focused on Sicilian material), or (ii) to be a synonym of *‘E.’ falconeri* (Ambrosetti 1968). As already noted, *‘E.’ falconeri* and *‘E. melitensis’* were never originally erected on the basis of size (Busk 1867), and certainly not on a size discrepancy as considerable as that described by Vaufrey (1929). If these two Maltese species do represent a single taxon (Adams 1874, Ambrosetti 1968), then the question of priority and type-designation arises.

Falconer first described *‘E. melitensis’* to the British Association at Cambridge on the 6th October 1862, but the name and description – the two key criteria of availability under article 12.1 of the International Code of Zoological Nomenclature (‘the Zoological Code’) – did not appear in print until after Falconer’s death in 1865 (Busk 1867). The only record of Falconer’s presentation in the British Association Archives is in the *10 Year Index*, under ‘list of papers of which abstracts have not been received’ (Appendix 111, p.195). This notes the title as ‘On ossiferous caves in Malta’, but includes no further details (Isabel McMann, Radcliffe Science Library, pers. comm. 2008). An anonymous report in the popular magazine ‘The Parthenon’, published on the 18th October 1862, summarized Falconer’s presentation, and was reprinted in the posthumous edited volume of Falconer’s notebooks and correspondence (Murchison 1868). This is widely cited as the first ‘description’ of ‘*E. melitensis’* (e.g. Osborn 1942, Ambrosetti 1968). However, while ‘*Elephas melitensis’ is used,* it is accompanied by a description which is unlikely to be considered sufficient to render the name available (Svetlana Nikolaeva, International Commission for Zoological Nomenclature, pers. comm. 2008):

“The pigmy Elephant was an animal of remarkably small proportions; an

> *adult individual could not have exceeded the Indian Tapir in height and bulk, a creature not much larger than a full-grown Hog. Contrasted with the bones and teeth of an adult African Elephant the difference in size of these portions of its frame exhibited were most striking. But though so small, the skeleton agreed in every particular with one of greatest bulk. A series of harmonies ran through the two skeletons, one bone answering to another truly, and without ordinal or generic difference. The author could refer it unhesitatingly to his subgenus Loxodon, in the African group of elephants."* (Anon. 1862, p.780)

'*Elephas melitensis*' is used in Spratt's May 1867 account of Zebbug Cave, but again, as no description accompanies the name, it is not made available. A month later, in June, Busk (1867) included Falconer's description (and attributed specimens) of *'E. melitensis'* in his own publication on the Zebbug Cave elephants. This same description of *'E. melitensis'* is reproduced in Falconer's Memoir and published notes (Falconer 1868, edited by Charles Murchinson). Busk places Falconer's text in quotation, and appends any dissenting opinion in his foot-notes. He then attributes the same specimens as Falconer to *'E. melitensis'* (in the text and figure legends), as well adding additional material to the *'E. melitensis'* hypodigm. This creates a perplexing priority dispute if *melitensis* and *falconeri* need to be synonymized on systematic grounds (are 'subjective synonyms'); the first clear descriptions, with referred and figured material, of both species, occur in Busk (1867).

Busk (1867) clearly treats *'E. melitensis'* as the senior name, and attributes authorship of that taxon to Falconer, however there is no objective way of identifying priority (page priority is not recognized by the Zoological Code). This matter has been further complicated by Osborn (1942) omitting any mention of the publication of Falconer's notes in Busk (1867), leading to a later assumption by many authors that *'E. melitensis'* was not described until 1868, and is thus a junior synonym of '*E.' falconeri*. Osborn (1942) fixed the lectotype of *'E. melitensis'* as NHM specimen number 44312, but for '*E.' falconeri* he referred to the published plates (XLIX, L and LI) in Busk (1867), which also includes specimens Busk attributed to *'E. melitensis'*. The types of *'E. falconeri'* therefore have not been fixed beyond the type series identified by Busk. Ambrosetti (1968) acknowledged the probable synonymy of these taxa, and the priority of *'E. melitensis'*. However, he argued that *'E.' falconeri* should continue to be used for the smallest elephants of Sicily, citing common usage and taxonomic stability as justifications. Ambrosetti (1968) also implied that formal judgement was being sought from the International Commission of Zoological Nomenclature (ICZN) on the validity of *'E.' falconeri,* and the insertion of *'E. melitensis'* on the list of invalid names. There are no records of this having occurred (ICZN 2007). The earliest reference I have found that has not previously been implicated in this priority debate is Lydekker's (1886) *Fossil Mammalia in the British Museum (Natural History), Part 4*, where Lydekker explicitly includes *'E'. falconeri* material within *'E. melitensis*', and considers them a single taxon:

> *"The typical form of this species* ['E. melitensis'] *is estimated to have*

> *occasionally attained a height of five feet, while the smaller form (to which Busk assigned the name* E. falconeri*) was only about three feet in height."*
> (Lydekker 1886, p.151)

As published catalogues are accepted as valid publications by the Zoological Code, Lydekker (1886) can be identified as the first reviser of these species. *'E. melitensis'* therefore has priority. Clearly, the discussion must return to first principals, establishing whether taxa are valid, as per their original description; then if they are synonymous; and finally, if Sicilian material is also referable to that taxon. Only then can one weigh up the relative merits of priority and common usage following the guidelines in the Zoological Code (articles 24.2 and 23.9.1).

4.1.2. Dwarf elephants as taxa

Mediterranean dwarf elephants therefore pose three key systematic questions: (i) are dwarf elephant taxa 'good' species (relative to each other and to their mainland ancestor); if so, (ii) how many dwarf elephant species are there, and (iii) which mainland taxa are their likely ancestor(s)? To be able to address questions two and three appropriately, question one must be considered as part of a wider discussion of species concepts, which inform species delineation and underpin evolutionary hypotheses.

Species concepts and species identification

The identification and delimitation of species are perennial problems for neontologists and palaeontologists alike (Smith 1994, Winston 1999). The desire to reconcile the operational concept of 'species' with its theoretical underpinnings as a 'real' biological and evolutionary unit, has generated a vast body of literature (e.g. Sites & Marshall 2003, and references therein). Consensus is far from being reached, and the increasing interest in molecular taxonomy and DNA barcoding has re-ignited debate as to how species ought to be defined, and thus identified (Vogler and Monaghan 2007, DeSalle *et al.* 2005).

The major tension between operational taxonomy (the 'business' end of species identification) on one hand, and evolutionary biology on the other, is the difference in emphasis between pattern and process (Smith 1994). Describing diversity, be it morphological, behavioural or genetic, is an empirical, pattern-driven exercise, while interpreting how this diversity evolved requires the consideration of evolutionary and biological processes. Traditional alpha-taxonomy recognises species based on diagnostic morphological characteristics, and thus is pattern-driven. Species concepts of the New Synthesis and later are heavily dominated by process: the biological species concept (*sensu* Mayr 1957, or the modified recognition species concept of Paterson 1985) and the evolutionary species concept (Simpson 1961, Wiley and Mayden 2000) are all process-based (Smith 1994). Phylogenetic species concepts (e.g. Wheeler and Platnick 2000, Mishler and Thierot 2000) are

pattern-based, with patterns identified through cladistic analyses rather than phenetic grouping (Smith 1994), but are also inherently process-linked as observed phylogenies are assumed to arise through evolutionary processes (with emphasis on monophyly), and characters coded accordingly. When phylogenies are produced from DNA sequence analyses, the resulting phylogenetic 'species', or molecular taxonomic units, are explicitly process-linked, and related to evolutionary species concepts (Vogler and Monaghan 2007).

Congruence between these approaches is far from perfect. Cryptic and polytypic species show that 'morphospecies' do not always correspond to a biological species concept, while biological species are not necessarily diagnosable (Mishler and Theirot 2000). Biologists concur that species arise through evolutionary processes, and their definition and delimitation ought to reflect this, but the logical end-point of such process-driven species concepts – molecular taxonomy – is untenable even to many evolutionary geneticists (e.g. Mallet and Willmott 2003). A strict, process-driven, DNA taxonomy might accurately describe molecular diversity, but widespread implementation is not likely to be feasible and would damage one of the key tenets of taxonomy: stability (Seberg *et al.* 2003). Thus the species debate turns full circle: if species are not circumscribed solely by their molecular – and thus their 'true' evolutionary/biological – diversity, how does one delimit a species? There is a growing consensus that DNA taxonomy ought to be used to describe the molecular 'hierarchical level roughly equivalent to the binomials of the traditional system' (Vogler and Monaghan 2007, p.3), and supplement, rather than supplant, traditional alpha-taxonomic methods that are rooted in morphology (Seberg *et al.* 2003, Wiens 2004, Wills *et al.* 2005).

For palaeontologists, this welcome reversion to a consideration of the role of diagnosable morphological characters in the species debate, and how these 'morphospecies' relate to the underlying patterns of molecular diversity, mean that extinct taxa can continue to be incorporated into research on the evolution of the Earth's biota, on a par with their extant counterparts. However, the species 'problem' remains unresolved. If species are more than arbitrary groupings of individuals, if they are 'real' biological and ecological units, then how are their limits circumscribed? In palaeontology, the desire to identify taxa that are equivalent to neontological species reflects this recognised special status of species as a real unit involved in macroevolutionary processes. The species is not just another taxon to be defined by a clustering (hierarchical or phenetic) of specimens with an arbitrary cut-off. Instead, the 'cut-off' level for the grouping of extinct organisms is often linked to observed patterns of variation in extant taxa (Cope & Lacy 1992, Cope 1993, Baab 2008), paralleling current approaches in molecular taxonomy which attempt to establish the degree of molecular variation consistent with described species (Sites & Marshall 2003, Vogler & Monaghan 2007).

The 'species problem' writ small

Disentangling concepts of pattern and process is also key to resolving dwarf elephant taxonomy

and systematics. Dwarf elephant fossils are found in abundance on many Mediterranean islands (Figure 3.1). As these islands, with the exception of Malta and Sicily, are not thought to have been contiguous since the Messinian Salinity Crisis (approximately 5.3 Ma; Marra 2005), and dwarfing is a recognized insular evolutionary phenomenon, fossils from different islands are considered to represent parallel evolutionary lineages, and are distinct taxa. This argument can be made without recourse to morphological analysis as it is process-based: we infer that there was no inter-breeding among geographically isolated taxa, in line with biological species concepts (*sensu* Mayr 1957). The situation is more complicated when considering the number of dwarf taxa present within an island (or putative palaeo-island such as Sicily and Malta) over time, where, in the absence of geochronological evidence, empirical methods alone must be used to delimit taxa (section 3.5.1). In this respect, dwarf taxa reflect the wider problem of species identification and delimitation in palaeontology: it is the 'species problem' writ small, further complicated by problems specific to parallel phyletic evolution.

Parallel evolution, homoplasy and phyletic species identification

Mediterranean dwarf elephant taxa are thought to share the same, or closely related, mainland ancestors (Palombo 2001a; Palombo 2003; Palombo & Ferretti 2005). Such close taxonomic affinity hampers the delimitation of dwarf taxa using cladistic methods, which rely on autapomorphy (or synapomorphy between individuals of the same species) to both delimit and diagnose a species: so far, morphological cladograms have been unable to resolve relationships between *Mammuthus*, *Palaeoloxodon* and *Elephas* at the generic level (Shoshani *et al.* 2007). Diagnostic characters unrelated to reduced body size may be difficult to identify in dwarf taxa, and as size in insular dwarfs is a homoplastic character it ought not be used to diagnose species (Mishler & Theirot 2000, Smith 1994). Inter-relationships are further complicated by the parallel evolution of dwarfism in each taxon: size change is accompanied by allometric shape change (Gould 1977; see Chapter 6), and thus other putative synapomorphic characters supporting conspecificity between dwarf taxa may actually result from a single homoplastic character, size. A strict phylogenetic species concept is therefore likely to group dwarf lineages of similar size, but from different islands and/or stratigraphical levels (i.e. independent dwarf lineages), erroneously into a single taxon. It is probable that only molecular data will provide robust phylogenetic support for species delimitation between such closely-related taxa, and ancient DNA preservation is unlikely in Mediterranean fossils (Smith *et al.* 2003; section 4.1.3).

Phenetic approaches to species identification

Phenetic methods allow assessment of the patterns of disjunction in size and shape among dwarf taxa without the need for identification of autapomorphy. Instead, they use analyses of trait variation to identify discrete clusters of individuals that are considered to constitute species (Smith 1994). Proponents of phyletic approaches for establishing species argue that 'phyletic species' are best suited for further analysis of evolutionary relationships using phylogenetic methods (Wheeler &

Platnick 2000, Mishler & Thierot 2000). Following similar logic, a 'phenetic species' is appropriate when further analysis is concerned with patterns of variation and trait evolution rather than the evolutionary relationships among taxa.

Phenetic clustering methods are also affected by potential allometric parallelisms, but allow for the exploration of the differing impact of size and shape on putative taxonomic groupings. When combined with contextual information on locality and stratigraphical position (Chapter 3), and a detailed study of allometry (Chapter 6), homoplasy may be teased apart from true apomorphies and allow for *post-hoc* identification of good diagnostic traits. Phenetic methods are also vital for understanding evolutionary trends beyond the resolution of morphological phylogenies, and are thus well-suited to investigating evolutionary patterns in closely-related taxa such as the Mediterranean dwarf elephants. Whether phenetic clusters conform to the rank of species is uncertain, however, and linked to considerations of intraspecific variation.

4.1.3. Intraspecific variation

The description and delineation of species in alpha-taxonomy recognizes and allows for intraspecific variation, but there are limits to how much variation is compatible with a single-species hypothesis. Understanding and controlling for the factors contributing to observed variation informs our expectations of the level of similarity and disjunction in morphological traits consistent with conspecificity. Variation can be partitioned into ontogenetic and static adult components, and further subdivided in to sexual, geographical and – in fossil taxa – temporal variation, as well as the expected idiosyncratic variation between individuals. Ontogenetic variation can be controlled for (Chapter 5) and, for the relatively small Mediterranean islands, within-island geographical variation is of little concern. Sexual dimorphism and temporal trends in variation are more difficult to deal with.

Sexual dimorphism

The predicted bimodal distribution of adult post-cranial variables within a size-dimorphic species can pose problems when deciding whether a sample contains one sexually dimorphic species, or two distinct, non-dimorphic, species. Overlap between distributions and the comparison with other dimorphic species is often used as evidence in support of sexual dimorphism (Plavcan & Cope 2001). We cannot, however, predict *a priori* the degree of sexual dimorphism in insular dwarfs, nor the degree of size divergence between species, and known dimorphic traits should not be used for taxonomic discrimination (Cope & Lacy 1995).

High levels of sexual size dimorphism are known in extant and extinct full-sized elephants (Moss 1988, Lister 1996b, Tassy 1996b, Sukumar 2003), with male elephants sometimes reaching twice the adult body mass, and 1.5 times the adult height of a female elephant (Hanks 1972, Laws *et al.* 1975). This size-dimorphism is reflected in the post-cranial dimensions of full-sized elephants

(section 5.3.4). It is reasonable to assume that dwarf elephant taxa will also exhibit sexual size dimorphism in their post-cranial dimensions, and this has been inferred from the Spinagallo Cave and Tilos dwarf elephants (Ambrosetti 1968, Theodorou 1983, Theodorou *et al.* 2007. Sexual dimorphism in dwarf elephants and the impact of post-cranial variation on taxonomy is explored in Appendix 5.

Despite considerable body size dimorphism, male and female elephant molars show little – if any – differences in size (Averianov 1996, Chang 2010, Roth 1992b), in line with other mammals (Gingerich 1981). We cannot be sure that dwarf elephant taxa will follow the same dimorphism patterns as full-sized elephants, and Tassy (1996b) has suggested that size variation in *Gompotherium angustidens* from En Péjouan could be explained by sexual dimorphism, suggesting the proboscidean trend is not straightforward. However, it seems unlikely that dwarf elephants would buck both the general mammalian trend and that of their close relatives. Comparison of dental and post-cranial variable distributions within an adult assemblage thus provides a test of dimorphism *versus* two species: a size-dimorphic mammalian species would be expected to show a bimodal distribution for post-cranial variables, but a unimodal distribution for dental variables. Bimodalism in dental variables would falsify a single species hypothesis. The absence of a bimodal distribution in post-cranial variables is not, however, evidence for a lack of sexual dimorphism. Assemblages may be taphonomically biased to single sex assemblages (Berger *et al.* 2001), and with small sample sizes, even non-overlapping male and female distributions can appear unimodal (Godfrey *et al.* 1993). Similarly, unimodal dental variable distributions are consistent with, but not proof of, the presence of a single species.

Temporal variation

The temporal dimension to palaeontological species is a perennial problem for species delineation in space and time. In a well-dated, well-stratified site, the time depth of a sample can be measured and the pattern of variation over time can be described, but there is no way of predicting temporal variation in a sample *a priori*. Increased time depth in a fossil sample might be expected to inflate sample variation (Plavcan & Cope 2001); however, stochastic evolutionary changes (e.g. drift) will not necessarily result in an increase in variation and, if selection variables vary over time, neither will adaptive change. In poorly dated, possibly time-averaged assemblages, the potential contribution of temporal variation is unknown.

The repeated insular dwarfing of elephants suggests a predictable directional change: large mainland taxa are dwarfed over time, and gradualistic models of evolution predict the presence of intermediate-sized individuals. At the same time, however, differing degrees of dwarfism in island mammals have been correlated with a number of ecological and environmental variables (e.g. island area, number of competitors, number of predators) (Case 1978, Heaney 1978, Lomolino 1985, Raia & Meiri 2006). Ancestor-descendent relationships should not, therefore, be inferred from size alone: in a time-averaged sample containing different-sized taxa, ‘intermediate-sized' dwarf elephants could be

the adaptive end-point of a phyletic lineage in their own right, or the ancestors of a smaller, crown taxon. In the absence of reliable geochronological evidence, or if one taxon could be ancestral to another (and thus part of the same dwarfing lineage), true evolutionary parallelism cannot be proven and must be allowed for in future analyses.

Discontinuity within a sample

Conspecifics are recognized by their similarity to one another, and dissimilarity to other taxa, regardless of whether the similarity criteria is morphological or genetic, or whether phyletic or phenetic inference is employed. In neontological taxa, discontinuity in the variation between taxa is generally of greater importance in species delineation than the total amount of intraspecific variance, which is often emphasized in palaeontological species (Gingerich 1985).

Patterns of discontinuity and observed intraspecific variance are, however, linked. The discontinuity observed between species is dependent on both their degree of relatedness and on the trait under study. When diagnostic traits are discrete, clearly definable and have no possible intermediaries, the limits of acceptable variation are clear: the absence of such diagnostic characters, or the clear modification of such a character to a different state, preclude conspecifity. However, in more closely related species, the perceived discrete nature of traits often breaks down, leading to intermediate character states, multi-state characters, and ultimately to quantitative, continuous measures of particular features. Patterns of discontinuity are therefore relative, with distantly related taxa being separated by large 'gaps' in morphology, measured in character states that already reflect larger amounts of evolutionary divergence.

Because discontinuity, even in continuous traits, is not expected to be high in very closely related species (Gingerich 1974), poorly-sampled assemblages may not identify distinct species clusters. Conversely, small sample sizes and poor sampling may produce the effect of 'discontinuity' within a single-taxon sample. Poor sampling and small sample sizes are characteristic of fossil samples. In these situations, an assessment of the amount of variation in that sample is useful as an arbiter in deciding whether the patterns of discontinuity are able to be accommodated within the 'typical' amounts of variation in a species.

The coefficient of variation (CV) provides a relative measure of variation in a sample and is size-independent (Sokal & Rohlf 1995, Plavcan & Cope 2001):

$$CV = \text{standard deviation}/\text{mean}*100 \qquad [4.1]$$

A size-independent measure is preferable to metrics such as range or variance, as larger measurements (taken on larger individuals) will be more variable in an absolute sense than small measurements (Simpson *et al.* 1960). Because biological variables tend to be normally distributed,

random sampling is more likely to select individuals close to the mean, and in small sample sizes this may result in biased values of CV (likely to under-estimate sample variation, as well as other metrics such as range) (Plavcan & Cope 2001). To counter this, CV is multiplied by Haldane's Factor (Haldane 1955, Sokal & Rohlf 1995):

$$CV_{(corrected)} = CV*[1+1/(4n)] \quad [4.2]$$

In palaeontology, CV is often employed as a metric for testing a single-species hypothesis: the CV of a fossil sample is compared with that of a 'good', usually extant, species (one-tailed F-test on the ratio of CV^2), and if significantly higher, a single-species hypothesis is rejected (Plavcan 1989, Martin & Andrews 1993, Plavcan & Cope 2001, Humphrey & Andrews 2008). This approach can be criticized on a number of grounds: (i) there is no conclusive evidence for a 'typical' amount of variation characterizing a species (Gingerich 1974), hence the test is heavily dependent on the comparative sample used, (ii) fossil species may be more variable than extant species, especially given the increased time depth of samples, and (iii) there is often overlap in the CV values calculated for a sample containing multiple species and that of a single-species sample, particularly if the species are closely related or of similar size (Cope 1993). However, it remains a useful way of objectively assessing the taxonomic importance of non-dimorphic morphological variation in a fossil sample, explicitly ties fossil species with neontological species (potentially fulfilling the criteria of 'equivalence' mentioned above), and in combination with multiple lines of evidence, may help to falsify a single-species hypothesis.

4.1.4. Revising dwarf elephant taxonomy

A phenetic approach to establishing a new, objective and robust taxonomy for Mediterranean dwarf elephants must consider variation in adult dwarf elephants (to control for ontogenetic variation) hierarchically within an island: firstly, at each stratigraphical level of each site; secondly, within each site; thirdly, between the equivalent stratigraphical levels of different sites; finally, the variation in the island as whole can be assessed (Figure 4.5). The hierarchy for testing single species hypotheses under this 'bottom-up' approach (Table 4.1) is dependent on the geochronological and palaeogeographic evidence discussed in Chapter 3, but makes no previous assumptions of taxonomic grouping. Instead, it assesses the conspecificity of individuals at increasing degrees of geographical and stratigraphical separation, mitigating the confounding effect of factors like sexual dimorphism.

Current species attribution and taxon validity

The 'bottom-up' approach to establishing phenetic species is systematically sound, and with no prior species designation the erection of new species names for each phenetic cluster would be

relatively straightforward. However, dwarf elephant species have already been described, and the material under study is attributed to named taxa. With the exception of the type-series (or lectotypes fixed by Osborn (1942) for each species, in which a species name is directly fixed to a specimen, this specific attribution has usually been based on the perceived diagnostic character of each taxon – size (section 4.1.1).

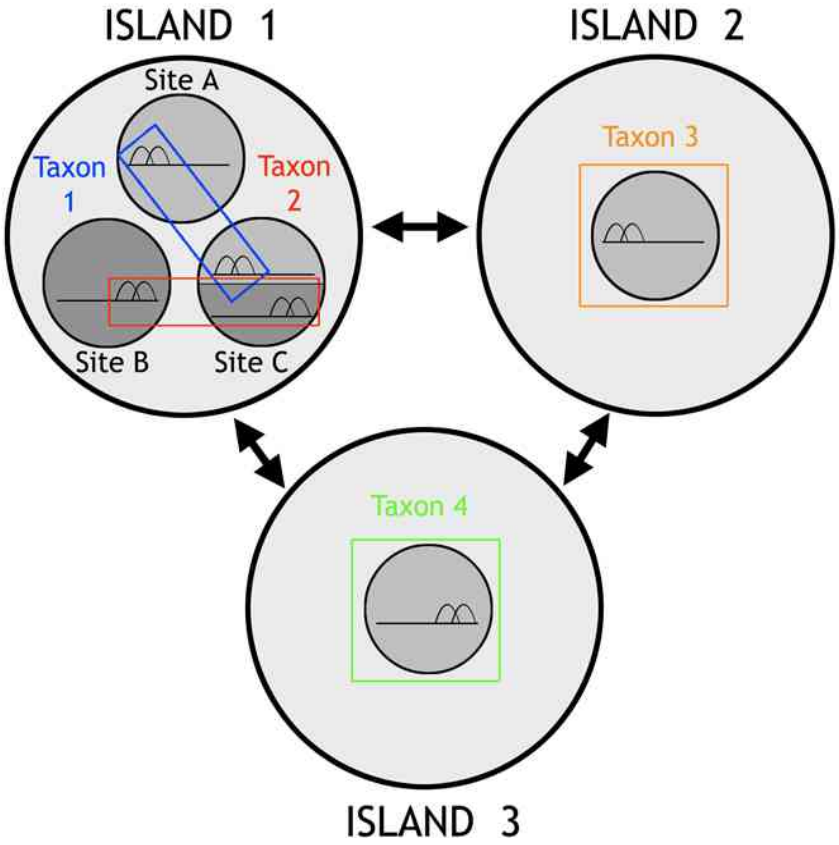

Figure 4.5. A 'bottom up' approach to dwarf elephant systematics and evolution. Trait variation is quantified for each stratigraphical level (e.g. Site C has two stratigraphical levels, dark and light grey) of each site within an island, creating "site-level' clusters of dwarf elephants. Overlapping bimodal distributions within a single site-level may be due to sexual dimorphism. Variation between sites is compared within and between stratigraphical levels. If there is no disjunction between site-level clusters, conspecificity between individuals cannot be rejected (e.g. Taxa 1 & 2 occur at two sites on Island 1). Once species are delineated (coloured boxes), traits can be compared between islands to investigate parallel evolution (taxa on different islands are discriminated from one another, even if their traits overlap

Island	Site	Stratigraphical provenance	Published Species	Island-wide geochronology	Hierarchy		
					1	2	3
Malta	Zebbug Cave (T)	None	*P. falconeri* (T) *P. melitensis* (T)	None			- -
	Mnaidra Gap (T)	co-occur in all fossiliferous layers	*P. falconeri?* *P. melitensis* *P. mnaidriensis* (T)				- - -
	Benghisa Gap	None	*P. falconeri?* *P. melitensis* *P. mnaidriensis*				- - -
	Gandia Fissure	None	*P. mnaidriensis*				-
	Ghar Dalam	all bone breccia ('Hippo layer')	*P. falconeri* *P. melitensis* *P. mnaidriensis*				- - -
Sicily	Spinagallo Cave	Layer 4	*P. falconeri*	Early-Middle Pleistocene			
	Luparello Cave	Layer 1 & 2* Layer 3*	*P. falconeri* *P. melitensis*				
	Puntali Cave	Layer 2* Layer 3*	*P. mnaidriensis* *P. mnaidriensis*	Middle-Late Pleistocene			
	Za Minica	Layer 4	*P. melitensis* *P. mnaidriensis*				
	Cavern di Carini	None	undescribed				
	San Teodoro Cave	Layer 2	*P. mnaidriensis*				
Crete	Cape Maleka (T)	None	*M. creticus* (T)	N/A		-	-
Cyprus	Imbohary (T)	None	*P. cypriotes*	N/A		-	-
Tilos	Charkadio Cave (T)	None	*P. tiliensis*	N/A		-	-

Table 4.1. Testing a single species hypothesis: bottom-up taxonomy. Contextual information (section 3.5) informs the hierarchy of hypothesis testing within an island: 1. within site, 2. sites grouped by geochronological age, 3. total island sample. The null hypothesis (H_0 = sample is a single species) is tested at each hierarchical level (samples grouped by grey shading). If H_0 is rejected at level >1, pair-wise comparisons between lower levels must be made. Note, grouping of specimens below the level of site (i.e. within-site stratigraphy) is not possible based on recorded information. Sites either have no stratigraphic division between specimens, no recorded stratigraphy or – where stratigraphic separation is indicated – the provenance of individual specimens is not recorded (*), preventing stratigraphical groupings. T denotes type localities (indicated for the site ,and the taxa it is the type locality for).

Following the tenets of the Zoological Code and good taxonomic practice, a second, complementary approach to dwarf elephant taxonomy can be followed. In contrast to the 'bottom-up' approach, this can be considered as 'top-down': constructing a valid taxonomic framework from published species identifications. This framework is based solely on the type, or referred, material of each species. Non-referred material from the same island – or island group – can then be compared with the name-bearing material, and assessed for conspecificity and inclusion in that taxon (Figure 4.6; Table 4.2). Any material not attributable to existing species must be designated a new species, and described as such.

'Top-down' and 'bottom-up' approaches are subtly, but fundamentally, different. 'Top-down' provides a test of the validity for the current taxonomy; 'bottom-up' identifies the number of taxa present, independent of this framework. Together they provide the basis of a robust taxonomy. In this chapter, I will attempt the first rigorous, pan-Mediterranean revision of dwarf elephant taxonomy using a combination of these approaches, assessing the homoplastic impact of dwarfism alongside species delimitation. I will identify the type material attributable to existing taxa and establish the validity of these named species. I will assess, again for the first time, the presumed synonymy between Maltese and Sicilian taxa. Finally, I will explore the probable generic affiliation, and thus ancestry, of dwarf elephant species. This will produce the most comprehensive taxonomic assessment of Mediterranean dwarf elephants to date.

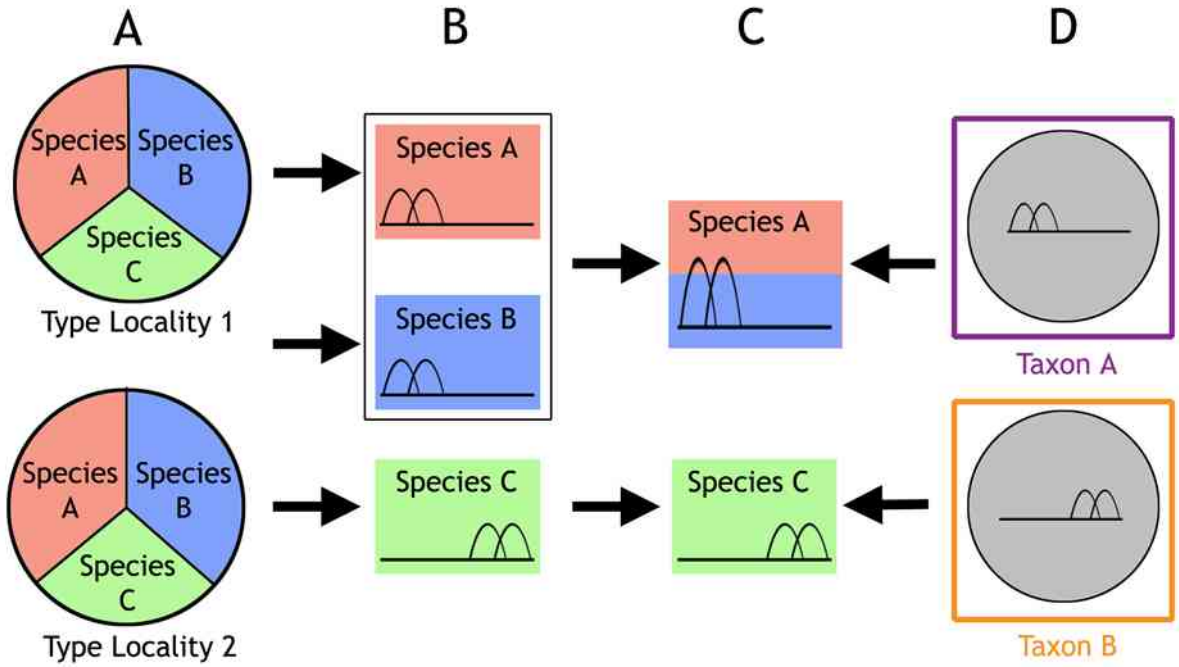

Figure 4.6. A 'top-down' approach to dwarf elephant taxonomy. Within each island, or island group, the validity and synonymy of existing taxa is assessed. **[A]** Type material for named species is identified from the original literature. **[B]** Trait variation in each type series is quantified. **[C]** If nominal taxa appear to be indistinguishable from one another (and no contextual data, such as stratigraphy, provide evidence against this), taxa are synonymized (e.g. Species A and Species B). The species name with priority is retained. **[D]** Material from other sites on the same island/island group, clustered using the 'bottom-down' approach, is then compared with the established name-bearing material, and attributed to the appropriate taxon, or – if necessary – assigned to a new species

Island	Described Species	Type Locality	Grouping					Malta			Sicily					
			1	2	3	4	5	Mnaidra Gap	Benghisa Gap	Ghar Dalam	Spinagallo Cave	Luparello Cave	Puntali Cave	Za Minica	C. di Carini	San Teodoro
Malta	*P. falconeri*	Zebbug Cave						X	X	X	X	X			?	
	P. melitensis	Zebbug Cave						X	X	X		X		X	?	
	P. mnaidriensis	Mnaidra Gap								X			X	X	?	X
Sicily	N/A	N/A														
Crete	*M. creticus*	Cape Maleka		-	-	-	-									
Cyprus	*P. cypriotes*	Imbohary		-	-	-	-									
Tilos	*P. tiliensis*	Charkadio Cave		-	-	-	-									

Table 4.2. Testing a single species hypothesis: top-down taxonomy. Taxonomic integrity of type-series is assessed within islands: first for each type-series singly (Grouping 1), then combined type-series samples (Groupings 2-5). The null hypothesis (H_0 = sample is a single species) is tested for each sample (constituent type-series grouped by grey shading). Once taxonomic integrity has been established (H_0 accepted for Grouping 1, rejected for all others), the validity of species attribution of specimens from other sites can be assessed. **X** indicates published species designation for material at each site (excluding type-series material); each site-sample can be compared with its respective type-series for conspecificity. If conspecificity is rejected, it is then compared with other named taxa within its island-group. If rejected as conspecific to all named taxa, it is designated a new species. **?** indicates no prior species attribution has been made. Note: Crete, Cyprus and Tilos samples comprise only material from the type locality. Consequently bottom-up and top-down taxonomy can be combined, as the type-series for each forms a subset of the total sample.

4.2. Materials and methods

Elephant taxonomy is heavily reliant on dental characteristics, and dwarf elephant taxonomy is no exception: four of the six described taxa in this study have teeth as type specimens. However, the type-series of *P. falconeri*, for which no lectotype has been fixed (Busk 1867), and the syntypes of *P. tiliensis* (Theodorou *et al.* 2007) include post-crania, as does the referred material of other dwarf taxa. Post-crania also provide valuable information on body-size trends. Sexually dimorphic traits should not be used for taxonomic discrimination (Cope & Lacy 1995), and t-tests and F-tests are sensitive to departures from normality (dimorphic traits are bimodally distributed) (Sokal & Rohlf 1995), thus dental characteristics provide the basis of the following taxonomic revision. Post-cranial variation is considered alongside dental variation and used to inform, but not establish, taxonomic validity. Cranial characters are also important in elephant taxonomy (Maglio 1973), but owing to time constraints, ongoing work by other authors on this material and the lack of cranial material in the type-series, they were not included in this study.

Molar and post-cranial morphometric measurements (Table 4.3) as well as qualitative dental characters (Table 4.4) were recorded for all sufficiently complete dwarf elephant and *P. antiquus* material studied for this thesis following the protocols describe in Chapter 2 (Tables 2.3-2.8). *M. meridionalis* data were obtained from Lister & van Essen (unpublished data) and Maglio (1973). *M. primigenius*, *L. africana* and *E. maximus* data were taken from Roth (1992b). *L. atlantica* and *P. iolensis* data were taken from Maglio (1973). All islands are treated independently in the first instance. As Sicily and Malta share a common taxonomic framework and geographical contiguity cannot be rejected on the current evidence, conspecificity must also be assessed between taxa from these islands.

4.2.1. Identification of types, type-series and referred material

Type-series are those specimens included in the original description, as designated by the author of that description. For example, the original description of *P. melitensis* by Falconer was published within Busk (1867), and while Busk (1867) also refers material to *P. melitensis* in the same work, this latter material does not form part of the type-series. Lectotypes fixed by Osborn (1942) are considered as the type for those species. All Maltese taxa were described prior to the material becoming accessioned into the NHM collection, and original type descriptions do not include the current specimen numbers. Only those specimens that could be reliably identified from the original description were included in the type series. These series were established through careful cross-referencing of original species descriptions (Busk 1867 (and Falconer therein), Falconer 1868, Adams 1874) with accession numbers in Lydekker's (1886) NHM catalogue, and through direct comparisons

Teeth	Ulna	Humerus	Tibia	Femur
Plate Count	Diaphyseal Length (DL)	DL	DL	DL
Length	Midshaft AP Diameter (MDAP)	Min. AP Diameter (MinAP)	MDAP	MDAP
Width	Midshaft ML Diameter (MDML)	Min. ML Diameter (MinML)	MDML	Max. MDML (Max_MDML)
Lamellar Frequency (LF)	Proximal AP Diameter (PAP)	PAP	PAP	PML
Crown Height	Proximal ML Diameter (PML)	PML	PML	DAP *
MinEst. Crown Height	Distal AP Diameter (DAP)	DAP	DAP	DML*
Hypsodonty Index (HI)	Distal ML Diameter (DML)	DML	DML	
Min. HI		Deltoid ML Diameter (DeltML)		
Av. enamel thickness				

Table 4.3. Dental and post-cranial parameters employed in this study. All measurements are in mm, except Plate Count, LF and HI. Details of measurements and indices in Chapter 2. Min. is minimum; Max. is maximum; Av. is average (for all specimens except *M. meridionalis* this is mean thickness (my data or from Maglio, 1973); *M. meridionalis* is modal thickness (Lister & van Essen, unpublished data)). Postcranial variables are logged for use in analyses.

	Character State		
Character	**0**	**1**	**2**
Medial Expansion	Absent	Present	
2^{o} Expansion	Absent	Present	
Enamel Figure	Lozenge- or cigar- shaped	Parallel-sided	
Enamel Folding	Unfolded	Lightly folded	Heavily folded
Early Wear Pattern	Equal or sub-equal loops	short-long-short loops	

Table 4.4. Qualitative dental characters employed in this study. Where molars were either too fragmentary or at an inappropriate wear stage for accurate character scoring, the character state was recorded as missing and not used to calculate character-state frequencies.

between published figures and NHM specimens. At the same time, locality information for each specimen was verified. *P. cypriotes* and *M. creticus* type-series were derived from Bate (1905) and Bate (1907), respectively, and *P. tiliensis* syntypes are listed in Theodorou *et al.* (2007). Identification of these type-series was straightforward, as the published species descriptions refer to accessioned material and specimen numbers are provided.

4.2.2. Identification of Operational Taxonomic Units (OTUs)

OTU is used here to refer to any phenetic group that conforms to a single species hypothesis, at any hierarchical level. An OTU is considered to be robust (and thus a good basis for species delineation) if it (i) forms a discrete cluster of individuals in bivariate and univariate plots of dental variables (no overlap with other OTUs), (ii) has CV values that are lower than that of a full-size comparator for at least one dental measure (see below) and (iii) is significantly different in mean values of dental variables from other OTUs. Minimum OTUs (mOTUs) represent the least inclusive grouping of conspecifics, either due to the rejection of a single species hypothesis at higher hierarchical levels, or to any contextual evidence suggesting a lack of conspecificity between phenetic groups, that can be combined without violation of a single species hypothesis. For example, the dwarf elephants of Luparello Cave and Spinagallo Cave could potentially have evolved on separate islands (Chapter 3), thus even if an analysis of a combined Luparello-Spinagallo sample did not reject a single species hypothesis, each site would continue to be treated as an mOTU despite a higher-level grouping being consistent with a single species hypothesis. Minimum OTUs are used in the consideration of potential size-related trends and patterns of post-cranial and qualitative trait variation. Only when these have been considered will final assessment of conspecificity between mOTUs be made.

Identifying phenetic groups

Phenetic clusters were identified from univariate and bivariate plots of upper and lower molar dental variables (molar width is treated as a proxy for tooth size and used as *x*-axis in all bivariate plots, allowing size-related trends to be assessed simultaneously). Samples were plotted to facilitate both top-down and bottom-up assessments: (i) Malta: points were colour-coded following their species attribution in Busk (1867), Falconer (1868) and Adams (1874). Type localities were plotted separately to allow visual assessment of both the type-series and individual sites simultaneously. Benghisa Gap and Gandia Fissure yielded too few specimens for clusters to be identified with any confidence at a single site, and were plotted together, along with specimens of unknown locality. Ghar Dalam was plotted separately owing to its large sample size; (ii) Sicily: points were colour-coded following their locality, and grouped into plots based on their island-wide geochronological groupings; thus phenetic clustering could be assessed simultaneously for hierarchical levels 1 and 2

(Table 4.1); (iii) Crete, Cyprus and Tilos: each island was plotted separately. All teeth (dP2-M3, and unidentified specimens) were plotted to qualitatively evaluate the potential for species delineation in pre-M3 teeth.

Size-independent sample variation: the coefficient of variation (CV)

Summary statistics (mean, minimum, maximum and CV) were calculated for plate count, length, width, lamellar frequency (LF), crown height, minimum crown height and enamel thickness of lower and upper M3s in *P. antiquus* and *M. meridionalis* and dwarf elephant type-series and site assemblages following Tables 4.1 & 4.2, and compared with literature values for *M. primigenius*, *L. africana* and *E. maximus* (Roth 1992b).

CV values for full-sized elephant species provide a 'yard-stick' by which the amount of variation in dwarf elephant fossils can be assessed. A single-species hypothesis is rejected if the CV of the dwarf elephant fossil sample is significantly higher than that of the full-sized comparator (one-tailed F-test of sample CV^2; $p<0.05$). These comparative samples, however, are not equivalent to each other in geographic or temporal range, and so differ in amount of 'species-level' variation. A higher comparative CV value provides a more conservative test for the presence of multiple taxa. This also increases the likelihood of type II error, and may be too conservative a test if variation results from measurement error rather than intrinsic species-specific variation. To help counter this, dwarf elephant CVs were compared with the CV values of all comparative samples to establish if rejection of a multiple-species hypothesis was comparator-dependent. However, the highest CV value was considered to be the only statistic that could reject a single species hypothesis, as (i) if dwarf CVs are not significantly higher than this value, then sample variation is within the observed range in 'good' elephant species and (ii), on the same basis, use of a lower value would ultimately reject a single species hypothesis for the other 'good' comparative taxa.

ANOVA of dental variables and post-hoc pair-wise comparisons

mOTUs identified within an island/island group were also compared for each dental variable using ANOVA and post-hoc comparisons of taxon pairs in JMP 7.0 (t-test, $P<0.05$), for both site-level and putative taxonomic groupings. If taxon/site pairs could be shown to be (i) significantly different in mean value and (ii) more variable than a single taxon sample when combined, and (iii) OTUs formed discrete phenetic clusters, this was taken as strong evidence for the rejection of a single species hypothesis.

Qualitative dental trait variation

Upper and lower M3 qualitative trait (Table 4.4.) character frequencies were calculated for each mOTU identified as above, and in *P. antiquus*, to identify potential diagnostic traits. Character states for *M. meridionalis*, *L. atlantica* and *P. iolensis* were inferred from the species diagnoses, figures and

plates in Maglio (1973). As character state frequencies were not recorded for these taxa, character states were scored as 'absent', 'sometimes present' or 'always present', or – for the semi-quantitative enamel folding – as 'always absent', 'absent or lightly folded' and 'lightly or heavily folded'. The frequency scores for dwarf elephant mOTUs and *P. antiquus*, obtained during the present study, were converted to this simple system to allow comparison. Frequencies were also compared between mOTUs to establish if character states supported grouping at higher hierarchical levels.

Size reduction trends as a taxonomic tool

Percentage size reduction in mean post-cranial (adult) and dental (M3) dimensions for each dwarf taxon (relative to putative mainland ancestor, see below) were compared within taxa (to identify evolutionary trends) and between OTUs identified as potential conspecifics by dental characteristics to establish if post-cranial dimensions supported conspecifity. Sexual dimorphism in post-crania causes size-reduction trends to differ between males and females, and were explored separately for putative sexes (identified in Appendix 5). Conspecifics are expected to be similar in both dental and post-cranial characteristics and will (i) cluster with each other on all dental and post-cranial characteristics, with no disjunction, except that compatible with sexual dimorphism (Appendix 5), and thus (ii) will show a similar ratio of dental to post-cranial size reduction.

4.2.3. Identification of size-related traits

The impact of allometry on phenetic grouping was explored through the identification of (i) size-related traits, and (ii) comparisons between independent dwarf lineages of the same size. Dwarf elephant samples were considered to be phyletically independent if they came from islands that were known to have been non-contiguous with each other during the Pleistocene. Post-cranial traits were assessed using principal components analysis (PCA) on a subset of dwarf elephant material to obtain an overview of total bone size-shape relationships (PCA variables in Table 4.3); and through bivariate analysis of distal femur AP and distal femur ML, to maximize dwarf elephant sample inclusion. A visual assessment of bivariate plots of principal component (PC) scores (PCs 1, 2 and 3) was made. PC1 was treated as a size and size-related shape axis, while PCs 2 and 3 were treated as shape axes (Jolicoeur 1963). Any separation on PC2 and PC3 was explored further to identify contributing variables (eigenvectors). As the aim here was to identify potential size-related traits that might affect taxonomic grouping, no further analysis was made on postcranial traits (allometric relationships are explored in Chapter 6).

Dental traits were not suited to multivariate analysis as wear stage and preservation limited the number of measurements common to multiple specimens. Instead, molar width was taken as a proxy for molar size, and used to compute size-corrected indices for each dental variable, except plate count and lamellar frequency (LF), in upper and lower M3s:

$$\text{variable index} = \text{variable/molar width}*100 \quad [4.3]$$

The size-index of crown height is the Hypsodonty Index. LF is a size-corrected index, albeit corrected using a different proxy of tooth size, in no further need of adjustment. LF also captures similar information to a size-corrected plate count index, and thus computation of this was considered redundant. mOTUs were grouped on the basis of size by pairwise comparisons of mean molar width (t-test, $P<0.05$; OTUs were considered of similar size if not significantly different in mean width). Index means were then (i) compared between mOTUs (t-test, $P<0.05$) and (ii) plotted against molar width for visual assessment of correlation with size. Size-related traits were those whose indices were (i) not significantly different between phyletically independent mOTUs of similar size, and/or (ii) showed a correlation between that index and molar width. mOTUs that could not be definitively identified as phyletically independent (i.e. those from the same island, or from Malta and Sicily) were still compared with each other, and size-related trait information was assessed for the amount of independent evidence for conspecificity: could all difference (or similarity) between these groups be attributed to size alone? Qualitative dental trait frequencies were also assessed for size-related trends. mOTUs were arrayed from lowest to highest mean M3 width (upper and lower molars considered separately), and trait frequency patterns visually identified from 100% stacked-column charts.

4.2.4. Generic affiliation of dwarf taxa

Size-corrected dental measures were also computed for full-sized mainland taxa *P. antiquus*, *M. meridionalis*, *P. iolensis* and *L. atlantica*, and compared with each other and dwarf mOTUs as per the identification of size-related traits. Traits that were shown to be size-independent, and genus-informative (i.e. could differentiate *Mammuthus* from *Palaeoloxodon*) were used to identify phenetic shape similarity between mainland and dwarf taxa, and thus infer generic affiliation. Qualitative dental traits (see above) were assessed for diagnostic power based on (i) character state variation in full-sized taxa and (ii) homoplastic dwarfing trends identified as per above. Congruence between phenetic groupings and informative qualitative traits was considered to provide additional support for generic affiliation.

4.3. Results

4.3.1. Full-sized comparative samples

CV values for lower and upper M3 variables differ between full-sized elephant species (Tables 4.5 & 4.6). Samples were not equivalent to each other in geographic or temporal range: *P. antiquus* material encompasses a broad geographic and temporal range (UK and Germany; 'Cromerian Complex' to Ipswichian, at least 400,000 years), whereas the *M. meridionalis* sample derives from a single region of Italy, the Upper Valdarno (dated ca. 2.0 - 1.77 Ma (Lister *et al.* 2005). *E. maximus* and *L. africana* samples, in contrast, encompass much smaller temporal ranges: spanning a few hundred years for *E. maximus,* while *L. africana* individuals consist of a contemporaneously culled population (Roth 1992b). *E. maximus* and *M. primigenius* samples both have large geographic ranges (Roth 1992b); the temporal range of the wooly mammoth sample is unspecified, but is likely to be within the last 50 ka (Lister pers. comm.) and can be assumed to have a greater time depth than the extant comparative material. The comparative samples can be ranked according to combined geographic and temporal range, which might be expected to correlate with species-specific values of CV (more variation expected in samples derived from geographically and temporally broad samples):

1. *L. africana*	<	2. *E. maximus*	<	3. *M. primigenius*	<	4. *M. meridionalis*	<	5. *P. antiquus*
single locality; 0 years		multiple sites, Asia; 100 years+		multiple sites, Russia; ca. 50 Ka		Upper Valdarno, Italy; ~ 250 Ka		multiple sites, N. Europe; 400 Ka+

Ranking of species by CV value is not consistent across variables, and only conforms to the above predicted order for one variable (lower M3 width). This may, in part, reflect differences in collection method: *P. antiquus* and *M. meridionalis* data were collected from isolated molars, whereas the literature data was, for the most part, taken on molars in the jaw bone. This is likely to have a greater impact on plate count and length measures: not all plates may be visible in the jaw, particularly in *E. maximus*, increasing measurement 'noise', while these measures are only taken on the most complete specimens of isolated molars, potentially exaggerating the difference in variance between fossil an extant samples. Roth (1992b, p. 193) indicates that measurements were taken on teeth that may have lost plates, or are not fully accessible for length measures, leading to inflated CV values, particularly for *E. maximus* (highest CV value for lower and upper M3 plate count and upper M3 length), and an overly conservative test for a single-species hypothesis. Plate count CVs are particularly variable, with *P. antiquus* and *M. meridionalis* showing considerably less variation than other taxa. As collection methods for these two taxa are known to be equivalent (personal observation, A. Lister pers. comm.), and a stringent inclusion criteria employed, this may reflect the lack of measurement noise, and may be a closer approximation of taxon-level CV in data collected by me for dwarf elephants. Ultimately, however, only the highest CV value can be used to falsify a

Species	Plate Count					Length (mm)					Width (mm)					Lamellar Frequency					Crown Height (mm)					Min. Crown Height (mm)					Enamel Thickness (mm)				
	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV
P. antiquus	13	18.5	18	20	3.6	5	377.6	340.8	390.8	5.8	25	76.5	60.0	90.5	11.5	24	4.8	3.8	6.9	16.7	8	160.9	148.1	175.0	7.0	8	151.2	135.0	185.0	11.6	23	2.0	1.5	2.5	13.2
M. meridionalis	12	13.0	11	14	8.2	13	282.6	250.0	335.0	11.2	26	96.3	76.5	115.0	10.7	24	4.8	3.6	6.1	12.4	7	120.3	92.0	147.0	16.3	0	.	.	.	.	24	3.1	2.2	4.3	16.4
*M. primigenius**	31	.	.	.	10.2	.	.	.	.	.	31	.	.	.	9.9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
*L. africana**	19	11.6	.	.	5.3	19	231.0	.	.	7.0	19	75.0	.	.	7.6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
*E. maximus**	6	26.2	.	.	13.2	6	377.0	.	.	6.5	6	83.0	.	.	8.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 4.5. Summary statistics of lower M3 dental measurements for full-sized elephant taxa. *M. meridionalis* from Lister and van Essen (unpublished data), * Data from Roth (1992b). Min is minimum, Max is maximum, CV is sample-size corrected coefficient of variation (Equation 4.2).

Species	Plate Count					Length (mm)					Width (mm)					Lamellar Frequency					Crown Height (mm)					Min. Crown Height (mm)					Enamel Thickness (mm)				
	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV
P. antiquus	14	18.3	16	20	6.0	7	291.7	245.3	332.6	12.5	22	80.1	69.0	92.0	9.6	26	6.2	5.4	7.4	11.0	11	168.5	140.0	194.0	11.7	9	170.0	147.0	231.0	17.2	21	1.9	1.6	2.4	10.8
M. meridionalis	23	13.0	12	15	5.9	17	259.7	220.0	330.0	12.4	34	97.4	74.0	121.5	13.8	33	5.4	4.5	6.4	11.1	19	121.5	104.0	146.0	9.4	0	.	.	.	.	29	3.1	1.7	3.7	15.9
*M. primigenius**	52	.	.	.	9.4	.	.	.	.	.	52	.	.	.	11.5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
*L. africana**	10	.	.	.	14.1	13	210.0	.	.	12.7	13	75.0	.	.	6.1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
*E. maximus**	8	23.3	.	.	20.0	8	279.0	.	.	21.6	8	82.0	.	.	5.5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 4.6. Summary statistics of upper M3 dental measurements for full-sized elephant taxa. Abbreviations as in Table 4.5. Note high CV for *E. maximus* plate count and molar length; Roth (1992b, p.193) suggests that these measures were taken on incomplete teeth, which might account for inflated CV relative to other full-sized taxa.

single hypothesis for any variable: the use of a lower value would logically also require comparator species (particularly the extinct taxa) with higher CV values to be rejected as a single species. While this may be a conservative test, any significant difference found provides a robust indication of multiple taxa within that sample. In addition, because data collection methods are not equivalent, mean lengths and widths are not comparable between all species: only *P. antiquus* and *M. meridionalis* can be directly compared with dwarf elephants for these measures when considering evolutionary trends. Data from Maglio (1973) is broadly comparable, but caution must be exercised during result interpretation.

4.3.2. Identification of type and referred material

Malta

Type-series of molar and long-bone material for the Maltese taxa *P. falconeri*, '*P. melitensis'* and *P. mnaidriensis* were identified from Busk (1867) and Adams (1874) (Appendix 6). Osborn (1942) fixed the types of *P. melitensis* (lectotype: NHM 44312 from Zebbug Cave; Figure 4.7) and *P. mnaidriensis* (lectotype: NHM 44304; paralectotype: NHM 44306, both from Mnaidra Gap; Figure 4.8), but did not designate a lectotype for *P. falconeri.*

The type-series of *P. falconeri* comprises just four teeth and seven long-bones, all from Zebbug Cave, Malta (Table A6.1). Of these, none are M3 teeth or adult post-crania, with the exception of one humerus, NHM 49253, which is fused distally but not proximally (and consequently possibly not fully-grown, see Chapter 5). This specimen, along with the unfused femur NHM 49260, and molars NHM 49239 and 40267, are also referred to *P. melitensis* by Falconer (in Busk, 1867; 1868) (Table A6.2). Busk (1867) also mentioned vertebrae, ribs, fore- and hindfoot bones, and fragments of pelvis, scapula and cranium in reference to *P. falconeri*. These were mostly juvenile and/or highly fragmentary. As the lectotypes of other Maltese taxa are molar specimens, this material was considered to be of greater interest for the comparative study of dwarf elephant anatomy; inclusion of all skeletal elements, for all taxa was beyond the scope of this thesis and this material awaits further study.

The first published description of '*P. melitensis'* by Falconer is found within Busk (1867), and includes an upper and lower M3 (NHM 49242 and NHM 44312, respectively). This was later republished, along with descriptions of the post-cranial material mentioned above, in Falconer (1868). The type-series of '*P. melitensis'* is thus considered to comprise the material described in Falconer (1868), while the authority for the species name remains Falconer (in Busk) 1867. Material from Benghisa Gap and Mnaidra Gap is referred to *P. melitensis* by Adams (1874). These do not form part of the original type-series, and the type locality for *P. melitensis* is therefore Zebbug Cave.

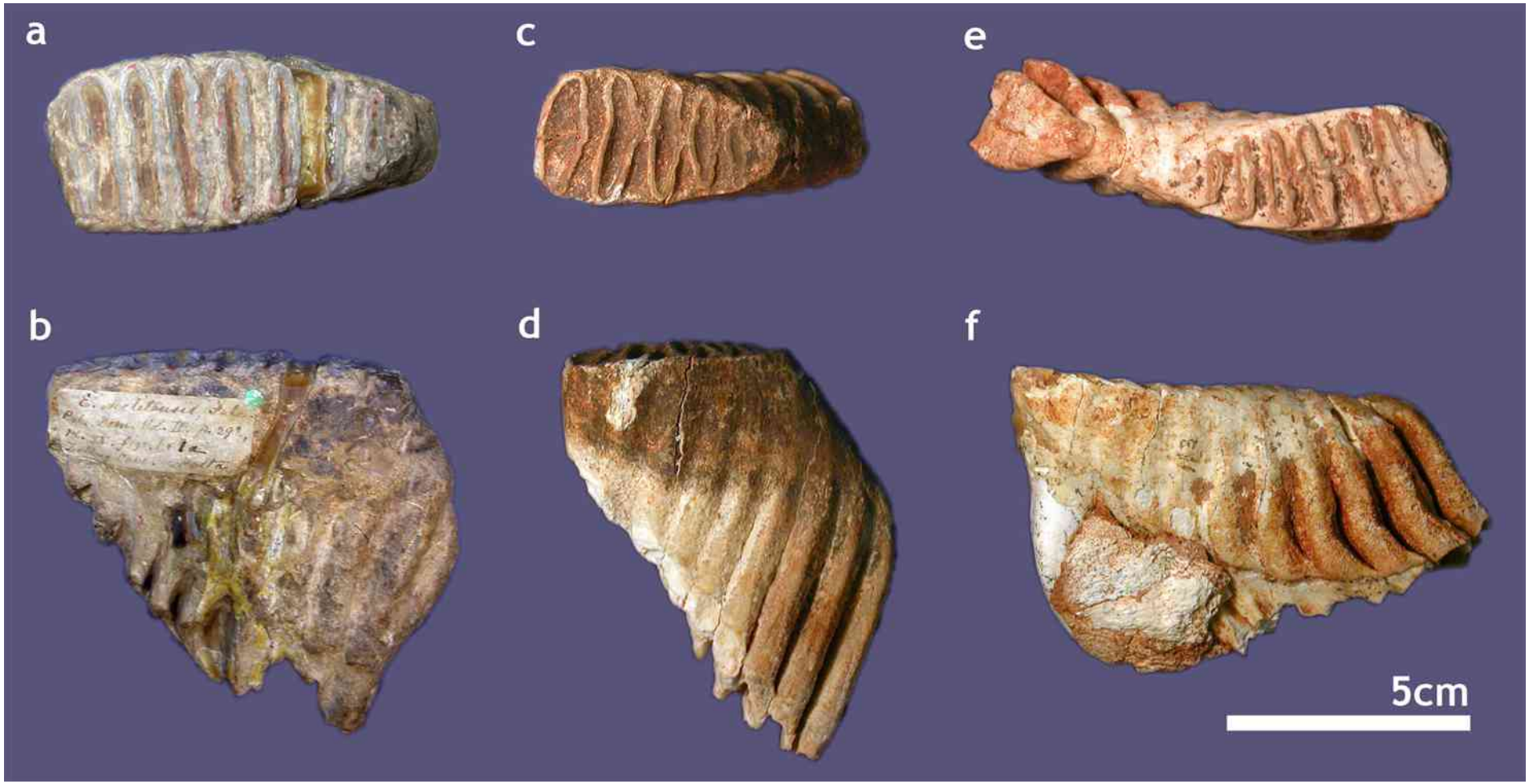

Figure 4.7. Lectotype of *P. melitensis* (Falconer (in Busk) 1867). [a] occlusal and [b] buccal view of NHM 44312 from Zebbug Cave, Malta, the specimen fixed by Osborn (1942) as the lectotype for *P. melitensis*. This specimen is a worn M^3, which has lost at least its anterior root to wear (it is worn into paired root region). As such, it has probably worn below its true maximum width and crown height. An upper [c & d] and lower [e & f] M3 from Spinagallo Cave, Sicily, are shown for comparison. The upper (no. 253) has its true front (only anterior talon lost to wear), but posterior plates are missing (producing the 'flat' back). The lower M3 also has its true front (only anterior talon lost to wear), and the anterior root is clearly visible, but is missing posterior plates. All three molars show an occlusal wear surface similar to *Palaeoloxodon* (medial expansion of enamel loop, 'cigar' shaped enamel loops in uppers and sub-equal loop patterns in early wear). Photo credit: the author.

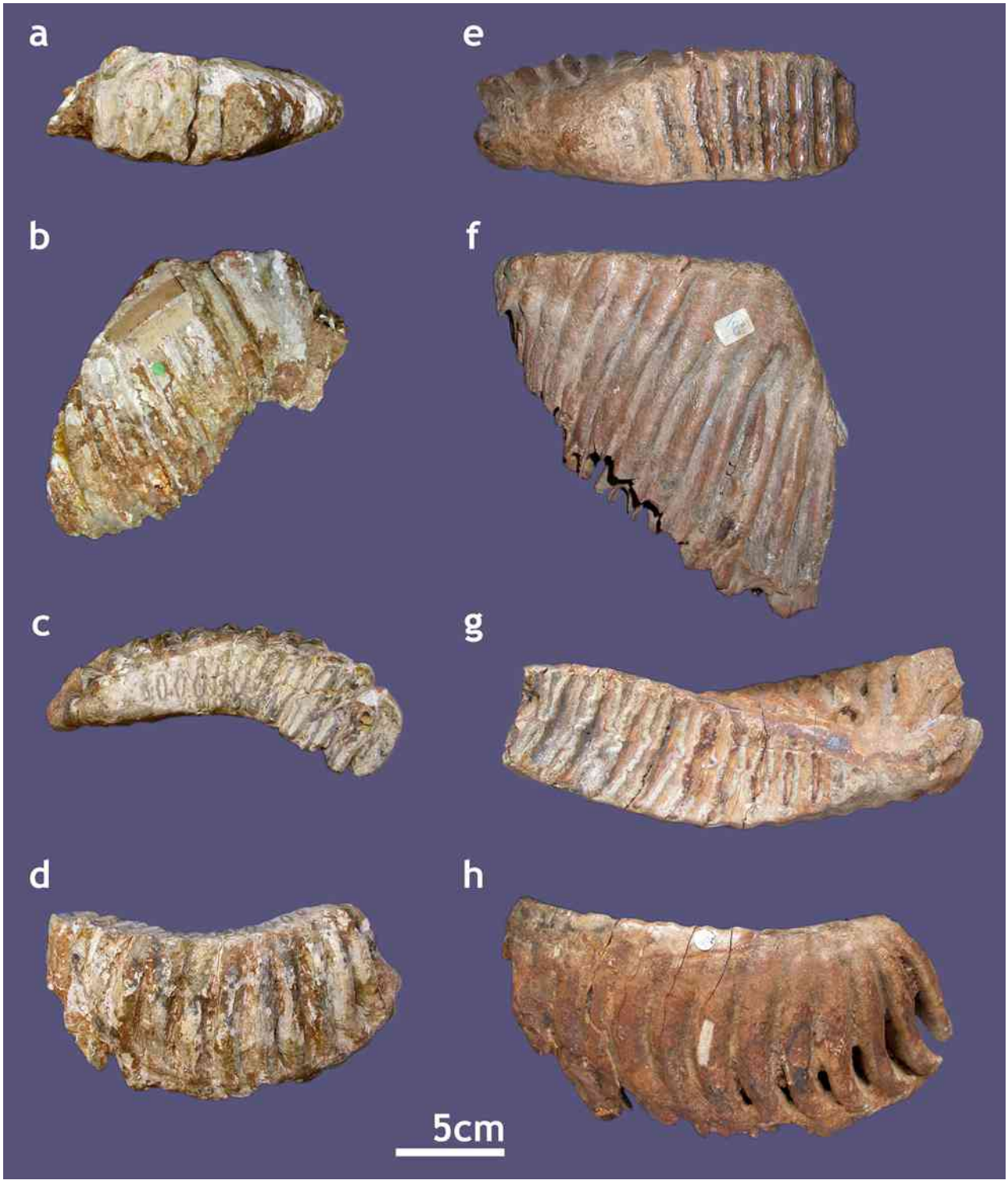

Figure 4.8. Lectotype and Paralectotype of *P. mnaidriensis* (Adams 1874). [a & b] Occlusal and buccal view of paralectotpe, NHM 44306. [c & d] Occlusal and lingual view of lectotype, NHM 44304, both from Mnaidra Gap, Malta. An upper [e & f] and lower [g & h] molar from Puntali Cave, Sicily, are shown for comparison. NHM 44304, though well worn, has its true front and back (anterior root present), whereas the Puntali Cave lower (no. 188/32) has lost its anterior to wear. NHM 44306 also appears to have its true front and back (although damage to the base of plates make this difficult to verify), whilst the Puntali Cave upper M3 (565/166) is missing at least its anterior root to wear. Photo credit: the author.

The type-series for *P. mnaidriensis* includes twelve M3 teeth and ten long-bone elements (mostly fragmentary, but with some measurements possible; Tables A6.3 & A6.4). Of the post-cranial material, 7 are adult specimens: NHM 44432, NHM 44433, NHM 44459 (femora); NHM 44430/8, NHM 44440 (tibiae); NHM 44377, NHM 44379 (humeri). The type-series for *P. mnaidriensis* comprises material from Mnaidra Gap, Benghisa Gap and Gandia Fissure, as well as material of unknown provenance within Malta. The lectotype and paralectotype (Osborn 1942) are both from Mnaidra Gap, designating this as the type locality for *P. mnaidriensis*.

Sicily

There are no species described from Sicilian material. Material from Spinagallo (e.g. Figure 4.7) and Luparello Caves are currently referred to *P. falconeri,* while material from Puntali (e.g. Figure 4.8), Za Minica and San Teodoro Caves is referred to *P. mnaidriensis* (Ambrosetti 1968, Palombo & Ferretti 2005, Bonfiglio *et al.* 2008).

Crete

The Cretan elephant material available for study was limited and fragmentary. The *M. creticus* type material was all excavated from a single locality, Cape Maleka, and a test for a single species at that locality is also a test of the validity of that taxon. The lectotype NHM M9381 was fixed by Osborn (1942) (Figure 4.9a&b). The large collection of dental material attributed to the large-sized elephant taxon *P. antiquus creutzburgi* stored at a regional museum in Rethymnon, Crete was not accessible, and pending inclusion of this material, the validity of this taxon is not addressed here. Instead, two 'large-sized' molars (Figure 4.9c&d) are included to allow exploration of size-related trends in phyletically independent lineages, and are referred to as '*P. antiquus* CRETE'.

Cyprus

The specimens from Imbohary, type-locality of *P. cypriotes* (Bate 1905), constitute the type-series for this taxon, and thus top-down and bottom-up taxonomic approaches are equivalent. The lectotype (NHM M8591) and paralectotype (NHM M8588) were fixed by Osborn (1942) (Figure 4.10).

Tilos

All *P. tiliensis* material was excavated from Charkadio Cave, Tilos, and a test for a single species at this site is also a test for the validity of this taxon. The majority of the *P. tiliensis* syntypes are post-cranial specimens (identified in Theodorou *et al.* 2007; syntype material UA T.3 (femur), UA T.339 (tibia), UA T.01.135 (tibia), UA T.01/239 (humerus), UA. T.41 (humerus) and UA T.01.198.u (ulna) were included in this study (square points, Figures A5.7 – A5.10). The molar syntype, UA T3272, was not available for study.

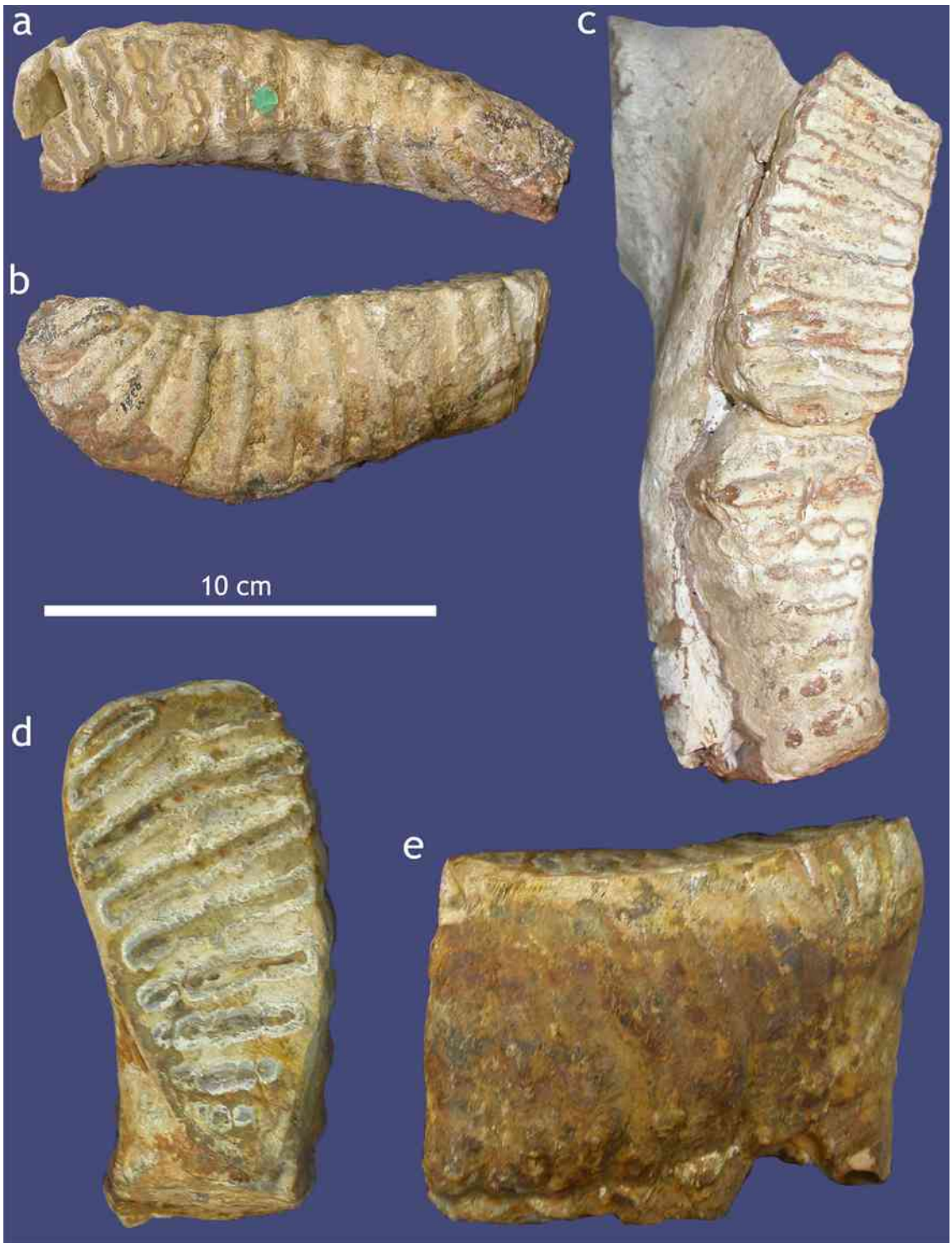

Figure 4.9. Cretan dwarf elephant molars. a. Occlusal and **b.** lingual views of M9381 (NHM), the lectotype of *M. creticus* (Bate 1907) from Cape Maleka. This specimen is a left lower M3. Note the low crown height, thick unfolded enamel. Small medial-expansion like bumps are visible on the first and second plates, but these vary in shape from the more triangular expansions seen in *Palaeoloxodon*. **c.** Occlusal view of M9384 (NHM), a fragment of the right mandible attributed by Bate (1907) to *P. antiquus*, from East Crete. Bate identified the teeth as dP4/M1 or M1/M2. The curve and taper in the rear tooth could, however, be indicative of M3 morphology; I have treated it as such for comparisons with 20.1.33, whilst acknowledging its uncertain identity. **d.** Occlusal and **e.** lingual views of 20.1.33 (NHM Crete), from Katharo Basin. This molar was attributed by Poulakakis *et al* (2002a) to *P. antiquus creutzburgi,* and identified as a right, upper M2. I identify this specimen as a left, lower M3, based on wear and curvature. The flattened back that Poulakakis *et al* took as evidence against M3 identification is due to the breakage and loss of posterior plates. Photo-credit: the author.

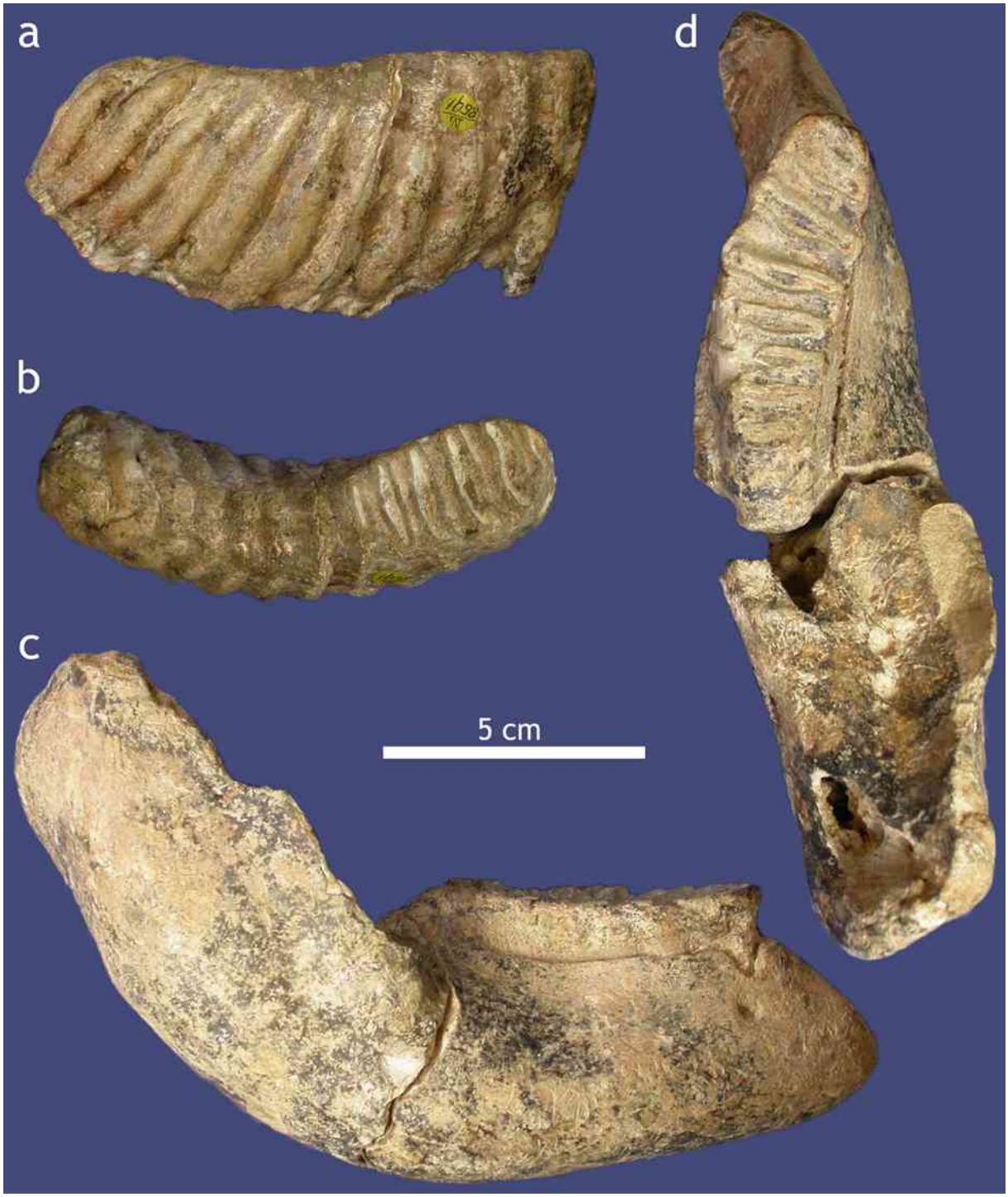

Figure 4.10. *P. cypriotes* type specimens. a. Lingual and **b.** occlusal views of NHM M8591, the lectotype of *P. cypriotes* (Bate 1905); a complete lower left M3 (anterior root and posterior talon are both visible). **c.** buccal and **d.** occlusal views of NHM M8588, *P. cypriotes* lectoparatype; a right mandibular ramus with M2 in wear. The early plates of the M3 had begun to form and are visible in **d.** (within the tooth alveolus). In both specimens note the relatively thick enamel, the unfolded enamel and absence of medial expansions. The enamel figure is lozenge or cigar-shaped. Photo-credit: the author

4.3.3. Phenetic identification of dwarf elephant OTUs

Validity of Maltese taxa

The CV values for lower M3 length, width, crown height and minimum crown height (Table 4.7), and upper M3 width, lamellar frequency and crown height (Table 4.8) in the total Maltese sample are significantly higher (F-test; P>0.05) than the highest full-sized comparator, and a single-species hypothesis for Malta can be rejected. The combined evidence of significantly high CV values for Mnaidra (lower M3 width and minimum crown height) and Benghisa Gaps (lower M3 width), where there are also two qualitatively observable clusters of M3s (Figure 4.11 c&e[2]), provides strong support for rejecting a single species hypothesis for these sites. CV values for all variables, from all sites, for upper M3s, are not significantly different from full-sized CV values (Table 4.8), and thus cannot reject a single species hypothesis. This is not at odds with the two-species signal from Mnaidra and Benghisa Gap lower M3s, however, as the upper molar sample appears equivalent in size range to the larger-sized of the two lower M3 clusters (Figure 4.11).

The presence of two discrete clusters corresponding to *P. melitensis* (red) and *P. mnaidriensis* (blue) type-series is clearly visible when Maltese M3s are plotted together (Figure 4.12). CV values for these clusters are compatible with a single species hypothesis, whereas the two groups combined are not (Tables 4.9 & 4.10; Malta 1 is equivalent to the *P. melitensis* hypodigm, whilst Malta 2 is equivalent to the *P. mnaidriensis* hypodigm), and are designated as putative taxa or OTUs, for further testing. Malta 2 lower M3 crown height CV is higher than the second highest full-size comparator, but this is not sufficient to reject a single species hypothesis. In addition, specimen NHM 44285 from Benghisa Gap, may have an artificially low crown height, increasing the sample CV: it was reconstructed from several pieces and its plates are highly 's-shaped' and lie at an oblique angle with respect to the occlusal surface, suggestive of some post-mortem distortion (pers. obs.).

In a combined Malta 1-Malta 2 sample, CV values for lower M3 width and crown height, and upper M3 lamellar frequency and minimum crown height, are significantly higher than the highest full-sized comparator CV (Tables 4.9 & 4.10), rejecting a single species hypothesis and indicating the samples should be treated as separate taxa. Malta 1 and Malta 2 are also significantly different in mean width, lamellar frequency and minimum crown height for both upper and lower M3s, as well as lower M3 crown height and enamel thickness (unpaired t-test; Table 4.11 & 4.12). The validity of *P. melitensis* and *P. mnaidriensis* is thus supported by three lines of evidence: (i) combined, the Maltese material referred to these taxa are more variable in key measures of tooth size than would be expected for a single elephant species, (ii) the material clusters into two, non-overlapping, size groups that correspond to the type-series for these taxa and (iii) mean values for several key molar variables are significantly different in these putative taxon groups.

[2] Figure 4.6e comprises Benghisa Gap, Gandia Fissure and unknown locality specimens; Benghisa Gap specimens are split between both M3 size-clusters

Site	Plate Count					Length (mm)					Width (mm)					Lamellar Frequency					Crown Height (mm)					Min. Crown Height (mm)					Enamel Thickness (mm)				
	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV
Zebbug Cave	1	11.0	11	11	.	0	.	.	.	.	3	34.1	33.1	35.4	3.7	3	9.1	8.0	10.0	12.2	1	49.5	49.5	49.5	.	1	66.2	66.2	66.2	.	3	1.6	1.5	1.6	5.8
Mnaidra Gap	1	13.0	13	13	.	1	186.9	186.9	186.9	.	6	37.6	26.6	50.5	31.6	5	7.1	5.4	8.7	21.7	1	84.5	84.5	84.5	.	4	62.9	46.3	75.8	24.6	5	1.5	1.2	1.8	17.6
Benghisa Gap	6	12.8	12	13	3.3	1	140.0	140.0	140.0	0.0	5	38.3	29.9	44.1	19.5	1	7.3	7.3	7.3	.	3	53.5	43.4	68.3	26.5	2	54.6	51.8	57.4	8.0	6	1.6	1.3	1.8	12.8
Ghar Dalam	2	13.5	13	14	5.9	2	189.3	155.1	223.5	28.7	10	56.9	46.6	64.6	9.5	14	6.3	4.6	8.2	16.8	2	110.5	108.0	113.0	3.7	7	100.1	84.7	112.4	9.2	11	1.7	1.4	2.0	11.3
Unknown Malta	0	.	.	.	.	0	.	.	.	.	1	46.5	46.5	46.5	.	0	.	.	.	.	1	95.5	95.5	95.5	.	0	.	.	.	.	1	1.9	1.9	1.9	.
All	10	12.8	11	14	6.4	4	176.4	140.0	223.5	22.3	25	45.2	26.6	64.6	26.7	23	6.9	4.6	10.0	20.7	8	76.4	43.4	113.0	38	15	78.3	46.1	112.4	30	26	1.6	1.2	2.0	13.2

Table 4.7. Summary statistics of lower M3 dental measurements for Maltese dwarf elephant localities. Min is minimum, Max is maximum, CV is sample-size corrected coefficient of variation (Equation 4.2). CV values that are significantly higher (F-test, P<0.05) than the highest (grey), second highest (orange), third highest (yellow), fourth highest (green) and fifth highest (blue) CV value observed for that measure in full-sized elephant taxa are shaded. Parameters shaded grey suggest more variation than is compatible with a single species hypothesis. Consideration of less stringent species-level CVs aims to minimize type II error (e.g. CV for *E. maximum* upper molar length seems inflated relative to other full-sized taxa, and may not represent a good 'yard-stick' for this measure). * denotes a 'combined' sample that actually comprises just one of the constituent groups, and thus statistics are not repeated. Malta 1 is equivalent to the type-series for *P. melitensis*, Malta 2 to the type-series for *P. mnaidriensis*. GD is Ghar Dalam.

Site	Plate Count					Length (mm)					Width (mm)					Lamellar Frequency					Crown Height (mm)					Min. Crown Height (mm)					Enamel Thickness (mm)				
	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV
Zebbug Cave	0	.	.	.	.	1	1	104.505	178	.	3	33.4	32.5	35.1	4.8	3	10.8	10.7	11.0	2.0	0	.	.	.	.	3	58.4	55.3	64.7	10.0	3	1.4	1.3	1.4	3.6
Mnaidra Gap	4	13.0	13	13	0.0	5	176.5	174.7	178.0	0.7	6	50.4	46.5	53.3	4.7	5	7.7	7.1	8.2	5.9	1	99.1	99.1	99.1	.	5	110.2	100.0	118.1	7.2	6	1.5	1.3	1.7	10.5
Ghar Dalam	1	14.0	14	14	.	1	176.0	176.0	176.0	.	3	65.3	58.0	76.0	15.8	6	7.3	6.6	8.2	10.4	4	142.6	124.7	160.0	11.1	2	121.5	112.5	130.5	11.8	6	1.8	1.5	2.0	12.3
Unknown Malta	1	13.0	13	13	.	0	.	.	.	.	4	43.3	36.0	49.0	14.6	4	9.3	8.3	10.9	13.1	3	91.6	73.8	102.2	18.4	0	.	.	.	.	3	1.4	1.2	1.6	14.9
All	6	13.2	13	14	3.1	7	166.1	104.5	178.0	16.4	16	48.2	32.5	76.0	23.8	18	8.4	6.6	11.0	18.0	8	118.1	73.8	160.0	26	10	96.9	55.3	130.5	29	18	1.6	1.2	2.0	15.3

Table 4.8. Summary statistics of upper M3 dental measurements for Maltese dwarf elephant localities. Legend as Table 4.7

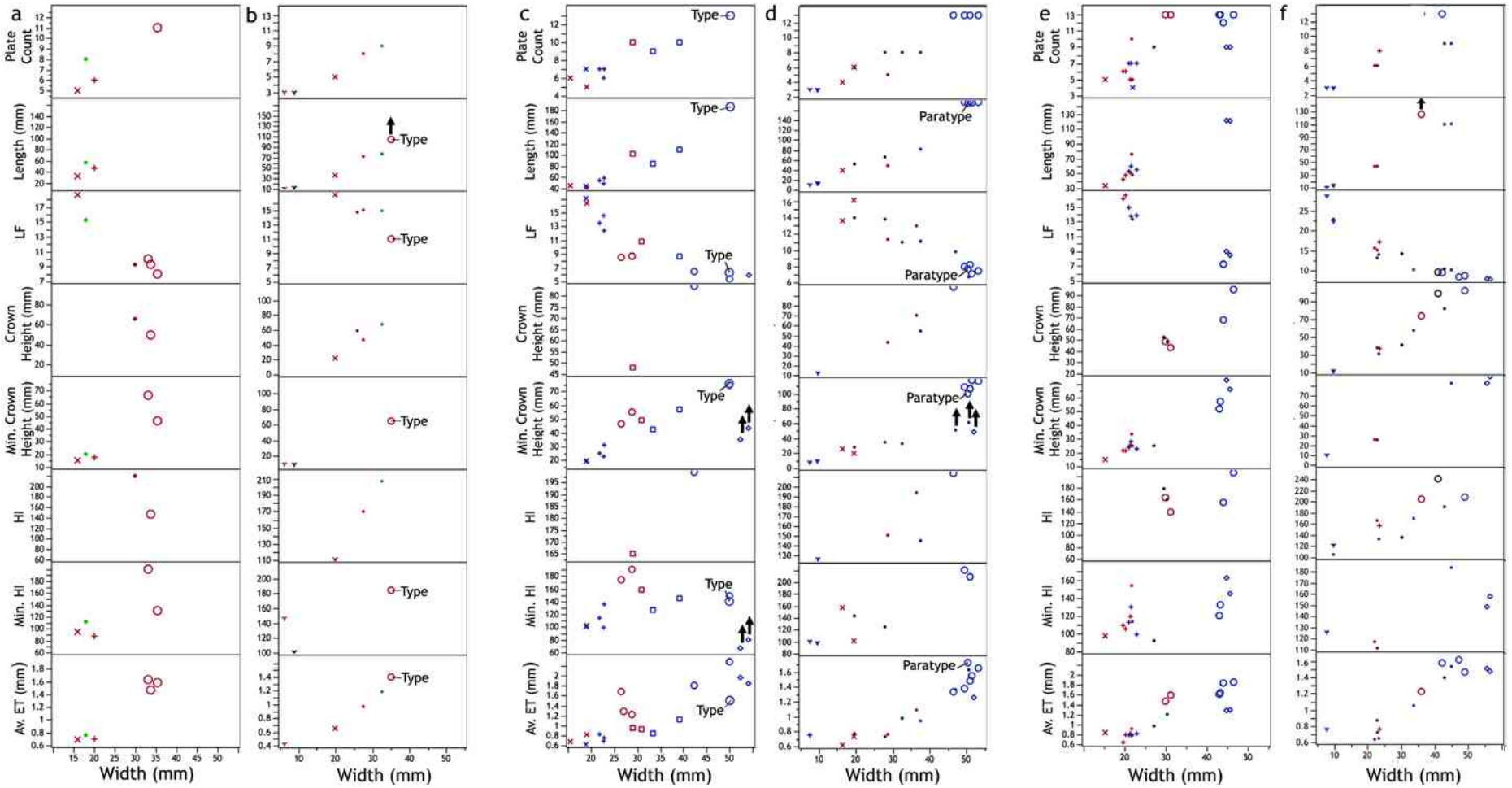

Figure 4.11. Bivariate scatter plots for Maltese elephant molars. Molar parameters are plotted against molar width for qualitative identification of clusters of individuals within sites and assessment of current taxonomy. Type series attribution following Busk (1867), Falconer (in Busk, 1867) and Adams (1874): '*P.* melitensis' (red), *P. mnaidriensis* (blue), *P. falconeri* (green) and *Elephas sp.* (black). Types fixed by Osborn (1942) for these taxa are labelled. Y, dP2; X, dP3; +, dP4; open squares, M1; open triangles, M2; open circles, M3; dots, uncertain identity. Tooth identification follows my designation, not that of the original type descriptions. **a.** lower and **b.** upper molars from Zebbug Cave; **c.** lower and **d.** upper molars from Mnaidra Gap; **e.** lower and **f.** upper molars from Benghisa Gap, Gandia Fissure and unknown locality. LF is lamellar frequency, HI is Hypsodonty Index, Av. ET is average enamel thickness. Min. Crown Height is a 'minimal' crown height taken from worn plates. Where this is considered to be a significant underestimate of true height, arrows have been added to individual points to indicate predicted 'true' position of point. Min. HI is HI calculated from Min. Crown height.

No support is found for another 'small-sized' taxon *sensu* Busk (1867): (i) there are only two observable discrete clusters of M3 specimens amongst referred material from Busk (1867) and Adams (1874) (Figure 4.12), and (ii) Zebbug Cave, the type locality for *P. falconeri* and 'P. melitensis', material cannot reject a single species hypothesis on the basis of CV (Tables 4.7 & 4.8). Pre-M3 teeth assigned to *P. falconeri* also show considerable overlap with other dwarf taxa, and are not resolvable into diagnostic groups (Figure 4.11 a&b). This follows the pattern in full-sized elephant taxa, where early teeth of different species are more similar in size, shape and plate number than later ones, and is suggestive of shared dental development (see Chapter 6). *P. falconeri* type-series material is thus non-diagnostic (juvenile limb-bones and pre-M3 teeth). The differences between this taxon and *P. melitensis*, perceived by Busk (1867) to justify the erection of *P. falconeri*, are not supported.

Taxonomic affinity of Ghar Dalam material

In the Ghar Dalam sample, there appears to be a single lower M3 outlier, separating from the main cluster on width (green open circles, Fig. 4.13e). Though the sample size is small, this individual also appears to separate on molar length, and is lower for all measures except plate count and minimum hypsodonty index relative to other Ghar Dalam lower M3s. Lower M3 length CV also rejected a single species hypothesis for Ghar Dalam (Table 4.7). The small sample of upper M3s from Ghar Dalam (n=3) is made up of two similar sized molars, and one larger specimen. As CV values for upper M3s were non-significant, and the sample size is small, this must conservatively be treated as sampling from differing regions of the normal range of a single species.

Conspecifity between Malta 1 and Ghar Dalam is rejected. CV values of upper and lower M3 width, crown height and minimum crown height and lower M3 length for a combined Malta 1-Ghar Dalam sample are significantly higher than the highest full-sized comparator (Tables 4.9 & 4.10). Mean values for width, lamellar frequency, crown height, minimum crown height and enamel thickness are also significantly different in lower and upper M3 from each of these groups, (Tables 4.11. & 4.12).

Conspecifity between Malta 2 and Ghar Dalam is also rejected, supporting the presence of a larger species in the Ghar Dalam material. Samples are significantly different in mean values of lower M3 width, crown height, minimum crown height and minimum hypsodonty index, and upper M3 width, crown height and enamel thickness (Tables 4.11 & 4.12). Minimum crown height CV for a combined Malta 2-Ghar Dalam lower M3 sample is also significantly higher than the highest full-sized comparative value (Table 4.9). Upper M3 width for this group is also significantly higher than the second highest comparative value (Table 4.10). However, the taxonomic separation of Malta 2 and Ghar Dalam material is less well supported than between Malta 1 and Malta 2, and Malta 1 and Ghar Dalam. Minimum crown height is taken from worn plates, and although inclusion criteria are stringent (values are only included if thought to be a good representation of true maximum crown height, based on the wear stage of the tooth), size difference, and thus combined Malta 2-Ghar Dalam CV, could be amplified. There is also overlap between Ghar Dalam and Malta 2 in key size-related variables (molar length, width and lamellar

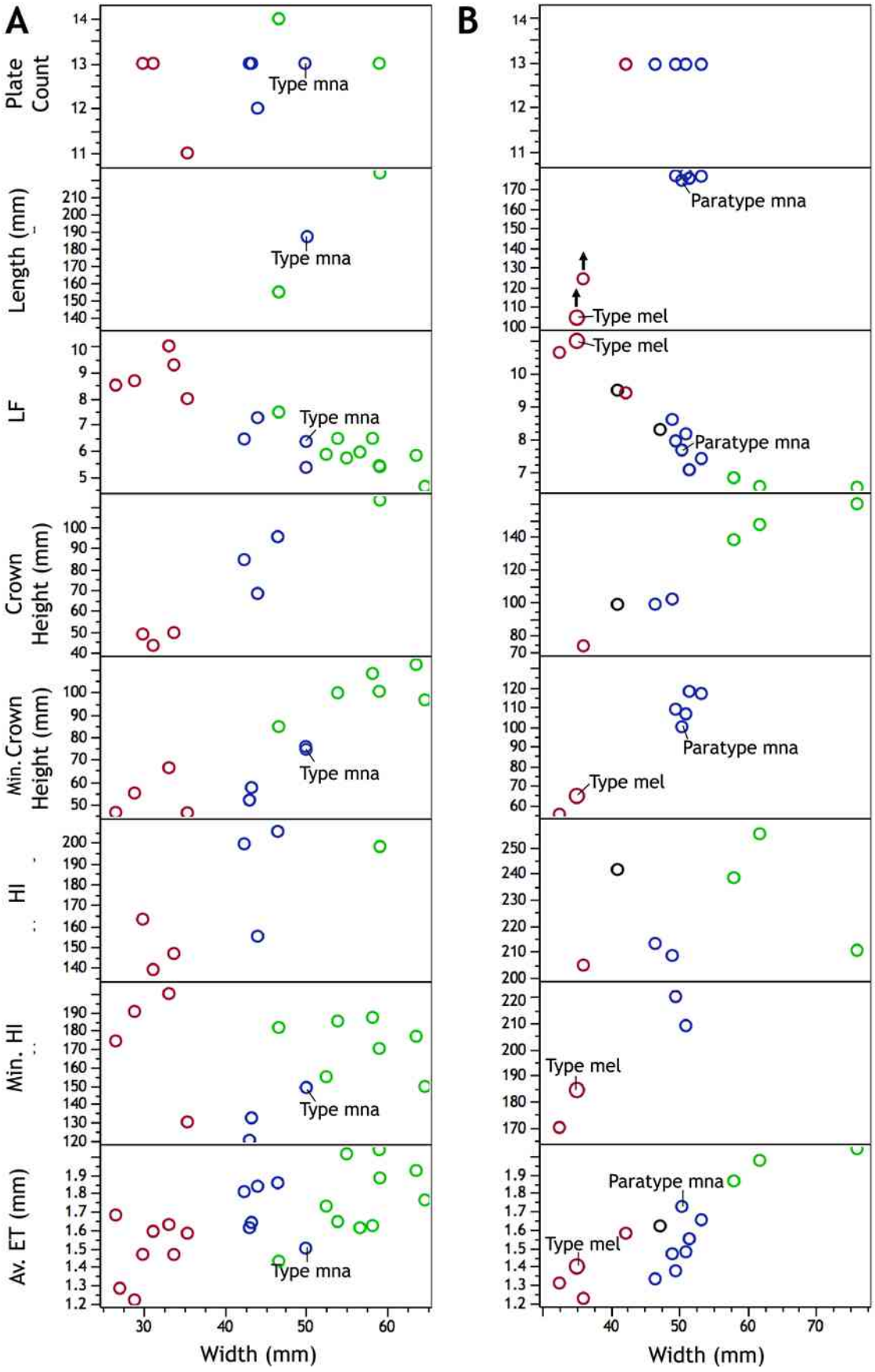

Figure 4.12. Bivariate scatter plots for Maltese M3 molars. [A] lower and **[B]** upper M3 molars from Malta. Red, '*P. melitensis*' type series; blue, *P. mnaidriensis* type series; black, *Elephas sp* (not Ghar Dalam); green, Ghar Dalam. Mel is *E. melitensis and* mna is *E. mnaidriensis*. Other abbreviations as Figure 4.6.

OTU	Plate Count					Length (mm)					Width (mm)					Lamellar Frequency					Crown Height (mm)					Min. Crown Height (mm)					Enamel Thickness (mm)				
	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV
Malta 1	4	12.5	11	13	8.5	1	140.0	140.0	140.0	0.0	8	30.7	26.6	35.4	10.7	5	8.9	8.0	10.0	9.2	3	47.2	43.4	49.5	7.7	4	53.4	46.1	75.8	18.98	9	1.5	1.2	1.7	12.1
Malta 2	4	12.8	12	13	4.2	1	186.9	186.9	186.9	.	7	45.7	42.4	50.5	7.7	4	6.4	5.4	7.3	13.1	3	82.8	68.3	95.5	17.9	4	64.9	51.8	75.8	19.87	6	1.7	1.5	1.9	8.8
Malta 1&2	8	12.6	11	13	6.1	2	163.5	140.0	186.9	22.8	15	37.7	26.6	50.5	22.5	9	7.8	5.4	10.0	20.2	6	65.0	43.4	95.5	34.3	8	59.1	46.1	75.8	20.5	14	1.6	1.2	1.9	12.1
Malta 1 & GD	5	12.8	11	14	9.0	2	189.3	155.1	223.5	28.7	18	45.3	26.6	64.6	31.5	19	7.0	4.6	10.0	21.7	5	72.5	43.4	113.0	36.4	11	83.1	46.1	112.4	30.9	19	1.6	1.2	2.0	13.6
Malta 2 & GD	6	13.0	12	14	5.1	3	188.5	155.1	223.5	19.7	17	52.5	42.4	64.6	14.0	18	6.3	4.6	8.2	15.6	5	93.9	68.3	113.0	20.3	11	87.3	51.8	112.4	23.1	17	1.7	1.4	2.0	10.2

Table 4.9. Summary statistics of lower M3 dental measurements for putative Maltese taxa. Legend as Table 4.7

OTU	Plate Count					Length (mm)					Width (mm)					Lamellar Frequency					Crown Height (mm)					Min. Crown Height (mm)					Enamel Thickness (mm)				
	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV
Malta 1	1	13.0	13	13	.	0	.	.	.	.	4	34.0	32.5	36.0	5.6	3	10.8	10.7	11.0	2.0	1	73.8	73.8	73.8	.	3	58.4	55.3	64.7	10.0	4	1.3	1.2	1.4	6.0
Malta 2	4	13.0	13	13	0.0	5	176.5	174.7	178.0	0.7	7	50.2	46.5	53.3	4.4	6	7.8	7.1	8.6	7.3	2	100.6	99.1	102.2	2.4	5	110.2	100.0	118.1	7.2	7	1.5	1.3	1.7	9.7
Malta 1&2	5	13.0	13	13	0.0	5*	.	.	.	.	11	44.3	32.5	53.3	19.3	9	8.8	7.1	11.3	17.9	3	91.7	73.8	102.2	18.4	8	90.8	55.3	118.1	31.3	11	1.4	1.2	1.7	10.7
Malta 1 & GD	2	13.5	13	14	5.2	1*	.	.	.	.	7	47.4	32.5	76.0	37.1	9	8.4	6.6	11.0	22.5	5	128.8	73.8	160.0	27.2	5	83.6	55.3	130.5	44.3	10	1.6	1.2	2.0	19.0
Malta 2 & GD	5	13.2	13	14	3.6	6	176.4	174.7	178.0	0.7	10	54.7	46.5	76.0	16.4	12	7.5	6.6	8.6	9.2	6	128.6	99.1	160.0	19.9	7	113.4	100.0	130.5	8.6	13	1.6	1.3	2.0	14.1

Table 4.10. Summary statistics of upper M3 dental measurements for putative Maltese taxa. Legend as Table 4.7

	Plate Count	Length (mm)	Width (mm)	LF	Crown Height	Min. Crown Height	HI	Min. HI	ET (mm)
ANOVA	<0.0001	0.0025	<0.0001	<0.0001	<0.0001	<0.0001	NS	0.0226	0.0001
Malta 1 vs Malta 2	NS	NS*	<0.0001	0.0028	0.0003	NS	NS	0.0085	0.0417
Malta 1 vs Ghar Dalam	NS	NS*	<0.0001	0.0002	<0.0001	<0.0001	NS*	NS	0.0061
Malta 2 vs Ghar Dalam	NS	NS*	<0.0001	NS	0.0054	<0.0001	NS*	0.0049	NS
Spinagallo vs Luparello 1	0.0386*	NS	NS	NS	NS	.	NS	.	0.0124
Spinagallo vs Luparello 2	NS	0.0246	<0.0001	NS	0.0024	0.0027	NS	NS	NS
Luparello 1 vs Luparello 2	0.0397*	0.0161	<0.0001	NS	0.014	.	NS	.	0.043
Puntali Cave vs Za Minica	NS*	.	NS*	NS*	.	NS	.	NS*	NS
Puntali Cave vs C. di Carini	0.0195	.	NS	NS	.	NS	.	NS	NS
C. di Carini vs Za Minica	0.0023	.	0.0178*	NS*	.	NS	.	NS*	NS
Spinagallo vs Puntali Cave	<0.0001	.	<0.0001	<0.0001	<0.0001*	<0.0001	NS*	NS	<0.0001
Spinagallo vs Za Minica	<0.0001*	.	<0.0001*	0.0021*	.	<0.0001*	.	NS*	0.0006*
Spinagallo vs C. di Carini	0.0006	0.0003*	<0.0001	0.0012	.	<0.0001	.	NS	<0.0001
Luparello 1 vs Puntali Cave	<0.0001*	.	<0.0001	<0.0001	<0.0001*	.	NS*	.	<0.0001
Luparello 1 vs Za Minica	<0.0001*	.	<0.0001*	0.0014*	.	.	.	.	<0.0001*
Luparello 1 vs C. di Carini	0.0002*	0.0003*	<0.0001	0.0009	.	.	.	.	<0.0001
Luparello 2 vs Puntali Cave	<0.0001	.	<0.0001	<0.0001	0.0019*	<0.0001	NS*	NS	<0.0001
Luparello 2 vs Za Minica	<0.0001*	.	<0.0001*	0.0036*	.	0.0001*	.	NS*	0.0014*
Luparello 2 vs C. di Carini	0.008	0.0018*	<0.0001	0.0032	.	0.0006	.	NS	0.0005
Malta 1 vs Luparello 1	NS*	NS*	NS	NS	NS	.	0.0118	.	0.0469
Malta 1 vs Luparello 2	NS*	NS*	<0.0001	NS	0.0041	0.0178	NS	NS	NS
Malta 1 vs Spinagallo Cave	NS	NS*	0.0148	NS	NS	NS	0.0373	NS	NS
Malta 1 vs Puntali Cave	<0.0001	.	<0.0001	<0.0001	<0.0001*	<0.0001	NS*	NS	<0.0001
Malta 1 vs Za Minica	<0.0001*	.	<0.0001*	0.0061*	.	<0.0001*	.	NS*	0.0003*
Malta 1 vs C. di Carini	0.001	0.0024*	<0.0001	0.0058	.	<0.0001	.	NS	<0.0001
Malta 2 vs Luparello 1	NS*	0.008*	<0.0001	0.0003	0.0012	.	NS	.	0.0004
Malta 2 vs Luparello 2	NS	NS*	NS	0.0014	NS	NS	NS	0.0195	NS
Malta 2 vs Spinagallo Cave	NS	0.0112*	<0.0001	0.0002	0.0002	0.014	NS	0.0002	NS
Malta 2 vs Puntali Cave	<0.0001	.	<0.0001	NS	0.0099*	<0.0001	NS*	0.0134	0.0024
Malta 2 vs Za Minica	<0.0001*	.	<0.0001*	NS*	.	<0.0001*	.	NS*	0.0106*
Malta 2 vs C. di Carini	0.0008	0.0342*	0.0007	NS	.	<0.0001	.	0.0031	0.0198
Ghar Dalam vs Luparello 1	0.0124*	0.0025	<0.0001	<0.0001	<0.0001	.	NS*	.	<0.0001
Ghar Dalam vs Luparello 2	NS	NS	<0.0001	0.0001	0.0007	<0.0001	NS*	NS	0.0688
Ghar Dalam vs Spinagallo Cave	NS	0.003	<0.0001	<0.0001	<0.0001	<0.0001	NS*	NS	0.0109
Ghar Dalam vs Puntali Cave	0.0002	.	0.017	0.0273	NS*	NS	NS*	NS	0.0012
Ghar Dalam vs Za Minica	<0.0001*	.	0.0068*	NS*	.	NS	.	NS*	0.0134*
Ghar Dalam vs C. di Carini	0.0386	0.0217*	NS	NS	.	NS	.	NS	0.0204

Table 4.11. ANOVA and t-test statistics for Maltese and Sicilian lower M3s. P-values for ANOVA and post-hoc least significant difference (LSD) test of significant difference in mean values of dental parameters in lower and upper M3s. The LSD test is equivalent to an unpaired t-test, but takes account of multiple comparisons in calculation of significance level. LF is lamellar frequency, Est. is estimated, HI is hypsodonty index, Min. is minimum, ET is enamel thickness. * Test-statistics calculated from a pair in which n=1 for at least one OTU, and may be unreliable (particularly non-significance). Note the low/non-significance of HI and Min. HI for all groups, suggesting that M3 teeth remain a similar shape (height:width) across dwarf taxa.

	Plate Count	Length (mm)	Width (mm)	LF	Crown Height	Min. Crown Height	HI	Min. HI	ET (mm)
ANOVA	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	NS	NS	<0.0001
Malta 1 vs Malta 2	NS*	.	<0.0001	<0.0001	NS*	<0.0001	NS*	NS	NS
Malta 1 vs Ghar Dalam	NS*	.	<0.0001	<0.0001	<0.0001*	<0.0001	NS*	.	0.0001
Malta 2 vs Ghar Dalam	NS*	NS*	<0.0001	NS	0.0003	NS	NS	.	0.0035
Spinagallo vs Luparello 1	0.0197	.	NS	<0.0001	NS	NS	.	NS	0.0006
Spinagallo vs Luparello 2	NS*	.	<0.0001	NS	0.001	.	.	.	NS
Luparello 1 vs Luparello 2	NS*	<0.0001	<0.0001	<0.0001	0.0002	.	NS	.	NS
Puntali Cave vs Za Minica	NS*	.	NS	NS	NS	.	NS	.	NS
Puntali Cave vs C. di Carini	NS	NS*	0.0261	NS	NS	.	NS*	.	NS
C. di Carini vs Za Minica	0.0223*	.	NS	NS	NS*	.	NS*	.	NS
Spinagallo vs Puntali Cave	<0.0001	.	<0.0001	<0.0001	<0.0001	<0.0001	.	NS	0.0095
Spinagallo vs Za Minica	<0.0001*	.	<0.0001	<0.0001	<0.0001	.	.	.	NS
Spinagallo vs C. di Carini	0.0019	.	<0.0001	<0.0001	<0.0001*	.	.	.	NS
Luparello 1 vs Puntali Cave	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	NS	NS	<0.0001
Luparello 1 vs Za Minica	<0.0001*	.	<0.0001	<0.0001	<0.0001	.	NS	.	0.0008
Luparello 1 vs C. di Carini	<0.0001	<0.0001*	<0.0001	<0.0001	<0.0001*	.	NS*	.	0.0001
Luparello 2 vs Puntali Cave	0.0004*	<0.0001	<0.0001	<0.0001	<0.0001	.	NS	.	0.0051
Luparello 2 vs Za Minica	0.0003*	.	<0.0001	0.0017	<0.0001	.	NS	.	0.0239
Luparello 2 vs C. di Carini	0.0223*	0.0012*	<0.0001	0.0043	0.0021*	.	NS*	.	NS
Malta 1 vs Luparello 1	NS*	.	0.0099	0.0282	NS*	NS	NS*	0.0165	NS
Malta 1 vs Luparello 2	NS*	.	0.0164	0.0115	NS*	.	NS*	.	NS
Malta 1 vs Spinagallo Cave	NS*	.	NS	NS	NS*	NS	.	NS	0.0036
Malta 1 vs Puntali Cave	0.0004*	.	<0.0001	<0.0001	<0.0001*	<0.0001	NS*	NS	<0.0001
Malta 1 vs Za Minica	0.0003*	.	<0.0001	<0.0001	<0.0001*	.	NS*	.	0.0011
Malta 1 vs C. di Carini	0.0223*	.	<0.0001	<0.0001	0.0004*	.	NS*	.	0.0007
Malta 2 vs Luparello 1	0.0139	<0.0001	<0.0001	<0.0001	0.0004	<0.0001	NS	NS	0.0322
Malta 2 vs Luparello 2	NS*	NS	NS	NS	NS	.	NS	.	NS
Malta 2 vs Spinagallo Cave	NS	.	<0.0001	0.0002	0.0018	<0.0001	.	.	NS
Malta 2 vs Puntali Cave	<0.0001	0.0003	<0.0001	0.0012	0.0001	0.0002	NS	NS	<0.0001
Malta 2 vs Za Minica	0.0001*	.	<0.0001	0.0282	0.0002	.	NS	.	0.014
Malta 2 vs C. di Carini	0.0014	0.0121	0.001	NS	0.0095*	.	NS*	.	0.0216
Ghar Dalam vs Luparello 1	0.0148*	<0.0001*	<0.0001	<0.0001	<0.0001	<0.0001	NS	.	<0.0001
Ghar Dalam vs Luparello 2	NS*	0.0002*	<0.0001	0.0022	<0.0001	.	NS	.	0.0262
Ghar Dalam vs Spinagallo Cave	NS*	.	<0.0001	<0.0001	<0.0001	<0.0001	.	.	NS
Ghar Dalam vs Puntali Cave	0.0082*	0.00167*	NS	NS	NS	NS	NS		NS
Ghar Dalam vs Za Minica	0.0023*	.	NS	NS	NS	.	NS	.	NS
Ghar Dalam vs C. di Carini	NS*	0.0414*	NS	NS	NS*	.	NS*	.	NS

Table 4.12. ANOVA and t-test statistics for Maltese and Sicilian upper M3s. See Table 4.15 for details/abbreviations.

frequency; Figures 4.14 & 4.15), although width underestimates are likely for the highly rolled and abraded Ghar Dalam material (pers. obs.; while only the most complete specimens were included, this material still fell short of the quality of other sites).

The rejection of a single species hypothesis for the material attributed to this site suggests that multiple taxa are present at Ghar Dalam (*P. mnaidriensis* and another larger taxon). Labels and records for Ghar Dalam material were damaged, destroyed or lost during the Second World War, and the sample currently attributed to Ghar Dalam Cave may include material from other Maltese localities (John Borg, pers. comm.), and this may account for the presence of multiple taxa. Reassessment of the original material for indications of preservation differences would be worthwhile in light of these findings. Molar variation thus supports the presence of three Maltese dwarf elephant taxa, differing to one another in size (plate count and hypsodonty indices show broad similarities, although Malta 2 uppers do appear less hypsodont; Figures 4.8 & 4.9): a 'small-sized' Malta 1 (= '*P. melitensis'*), a 'medium-sized' Malta 2 (=*P. mnaidriensis*) and a new large-sized taxon from Ghar Dalam.

Post-cranial variation in Maltese elephants

The adult material available for Maltese elephants comprises a small number of fragmentary specimens, and is not sufficient to identify species-clusters or sexual dimorphism trends. Material is grouped based on its species attribution following Busk (1867), Falconer (1868) and Adams (1874) (Table A6.4); no post-cranial material from Ghar Dalam Cave was included in this study (owing to its poor preservation). No species contains more than 2 specimens for each variable, and alone gives little insight into Maltese elephant diversity. When considered alongside Sicilian dwarf elephant post-cranial variation, the material assigned to *P. falconeri* and *'P. melitensis*' is consistent with a single, sexually dimorphic species, and the total Maltese post-cranial sample is consistent with the presence of two, different-sized elephant species (Appendix 5). This is in line with the phenetic groupings based on molar evidence.

Sicilian dwarf taxa

CV values for all Sicilian material combined reject a single species hypothesis (all lower M3 values, except plate count; upper M3 width, lamellar frequency, crown height and minimum crown height; Tables 4.13 & 4.14). In contrast, a single species hypothesis cannot be rejected for any Sicilian dwarf elephant locality, with the exception of Luparello Cave. As with Maltese data, pre-M3 teeth provide no evidence for taxonomic separation within or between sites.

Two M3 clusters, designated 'Luparello 1' and 'Luparello 2', separating on molar size (width, length and crown height) and enamel thickness, are apparent in the Luparello Cave sample, with the smaller-sized molars (Luparello 1) overlapping with the Spinagallo Cave sample (Figure 4.13). CV

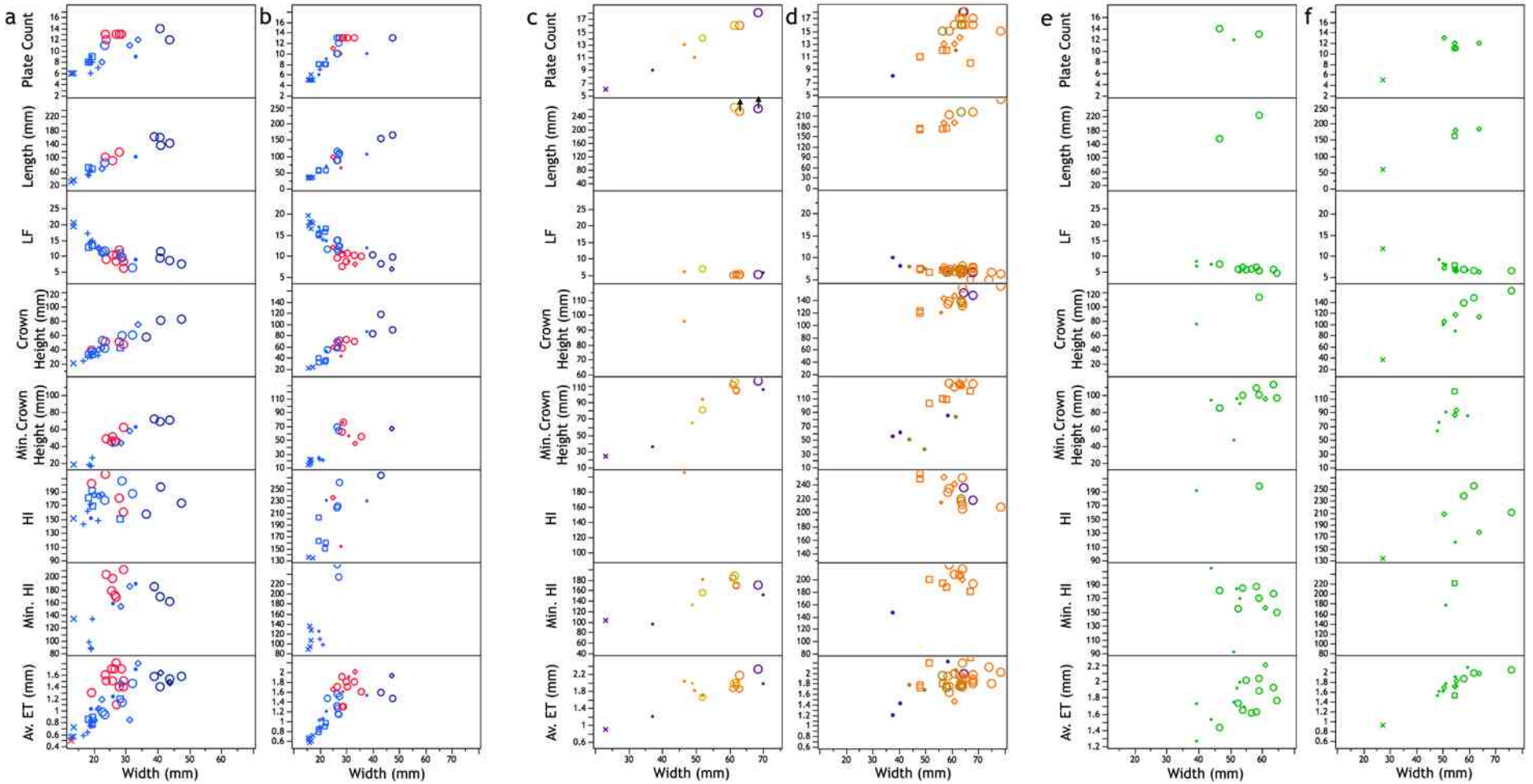

Figure 4.13. Bivariate scatter plots for Sicilian and Maltese elephant molars. Molar parameters are plotted against molar width for qualitative identification of clusters of individuals within and between sites. Symbols and abbreviations as in Figure 4.6. Sicily: **a** lower and **b** upper molars from Spinagallo (red) and Luparello (blue) Caves; **c** lower and **d** upper molars from Puntali Cave (orange), Za Minica (purple) and Cavern di Carini (yellow); Malta: **e** lower and **f** upper molars from Ghar Dalam (green). Note the two clusters of M3s in Luparello Cave material: 'larger' individuals (dark blue; labelled '*E. melitensis*' at the IPH) do not overlap in width with Spinagallo Cave, whereas 'small' individuals (light blue; labelled '*E. falconeri*' at IPH) do. Where measures are considered to be a significant underestimate, arrows have been added to individual points to indicate predicted 'true' position of point, e.g. length measures for Puntali Cave and Za Minica in **b** are taken from teeth missing their anterior root.

Site	Plate Count					Length (mm)					Width (mm)					Lamellar Frequency					Crown Height (mm)					Min. Crown Height (mm)					Enamel Thickness (mm)				
	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV
Spinagallo Cave	5	12.8	12	13	3.7	3	103.0	91.6	116.0	12.9	11	25.9	19.3	29.3	11.1	7	9.7	8.3	11.9	13.7	4	46.9	39.1	50.9	12.5	5	47.3	45.5	51.2	5.6	11	1.5	1.1	1.8	14.1
Luparello Cave	3	12.3	11	14	13.4	6	130.0	85.0	161.0	25.4	10	35.6	22.8	47.5	24.4	8	9.4	6.3	11.6	21.0	7	62.1	41.7	82.4	24.5	3	70.5	68.9	72.0	2.4	9	1.4	0.9	1.6	20.5
Puntali Cave	6	16.3	16	17	3.3	0	.	.	.	.	5	62.2	61.0	63.0	1.4	15	5.3	4.8	6.2	8.7	1	115.0	115.0	115.0	.	6	106.7	102.6	112.0	3.5	16	2.0	1.8	2.6	11.2
C. di Carini	3	15.0	14	16	7.2	1	266.0	266.0	266.0	0.0	2	56.8	52.0	61.5	13.3	2	6.0	5.1	6.9	22.7	0	.	.	.	.	3	98.9	81.0	115.0	19	7	2.0	1.6	2.4	15.0
Za Minica	1	18.0	18	18	.	0	.	.	.	.	1	68.5	68.5	68.5	.	1	5.1	5.1	5.1	.	0	.	.	.	.	1	116.4	116.4	116.4	.	1	2.3	2.3	2.3	.
All	18	14.6	11	18	14.2	10	135.5	85	266	40.5	29	39.1	19.34	68.5	40.6	33	7.3	4.8	11.9	33.1	12	61.4	39.1	115.0	35.8	18	83.4	45.5	116.4	33.3	44	1.8	0.9	2.6	21.8

Table 4.13. Summary Statistics of lower M3 dental measurements for Sicilian dwarf elephant localities. Min is minimum, Max is maximum, CV is sample-size corrected coefficient of variation (Eq. 4.2). CV values that are significantly higher (F-test, P<0.05) than the highest (grey), second highest (orange), third highest (yellow), fourth highest (green) and fifth highest (blue) CV value observed for that measure in full-sized elephant taxa are shaded. Parameters shaded grey suggest more variation than is compatible with a single species hypothesis. Consideration of less stringent species-level CVs aims to minimize type II error (e.g. CV for *E. maximum* upper molar length seems inflated relative to other full-sized taxa, and may not represent a good 'yard-stick' for this measure).

Site	Plate Count					Length (mm)					Width (mm)					Lamellar Frequency					Crown Height (mm)					Min. Crown Height (mm)					Enamel Thickness (mm)				
	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV
Spinagallo Cave	4	13.0	13	13	0.0	0	.	.	.	.	8	30.2	26.6	35.7	10.0	8	9.7	7.6	10.8	11.6	5	67.5	57.3	72.5	9.2	3	64.2	55.0	75.8	17.8	9	1.7	1.3	1.9	13.6
Luparello Cave	6	11.8	10	13	13.0	8	120.9	86.3	165.0	26.2	10	31.5	22.9	47.5	26.0	11	11.1	7.7	13.7	18.3	9	77.0	54.3	117.7	27.8	2	66.1	63.5	68.8	6.4	10	1.4	1.1	1.6	12.1
Puntali Cave	17	16.5	15	18	4.9	6	217.7	197.0	257.9	10.2	19	65.7	58.5	78.5	8.4	25	7.0	4.8	8.0	9.7	7	142.7	131.0	163.0	9.5	6	132.4	127.0	139.0	3.1	25	1.8	1.5	2.2	9.5
C. di Carini	2	15.5	15	16	5.1	1	221.2	221.2	221.2	.	3	59.3	56.5	63.5	6.7	2	6.9	6.5	7.2	7.8	1	139.4	139.4	139.4	.	0	.	.	.	.	5	1.8	1.6	2.0	6.9
Za Minica	1	18.0	18	18	0.00	0	.	.	.	.	2	66.3	64.5	68.0	4.2	2	6.6	6.5	6.8	3.6	2	150.0	148.0	152.0	2.1	0	.	.	.	.	1	2.0	2.0	2.0	.
All	30	15.1	10	18	14.8	15	166.3	86.3	257.9	34.4	42	50.3	22.9	78.5	36.0	48	8.3	4.8	13.7	25.8	24	102.9	54.3	163.0	37.6	11	101.7	55.0	139.0	35.8	50	1.7	1.1	2.2	14.1

Table 4.14. Summary Statistics of upper M3 dental measurement for Sicilian dwarf elephant localities. Legend as Table 4.13

values also reject a single species hypothesis for Luparello Cave (lower M3 length and width, and upper M3 width, lamellar frequency, and crown height; Tables 4.13 & 4.14). Separately, 'Luparello 1' and 'Luparello 2' cannot reject a single-species hypothesis for any variable (Tables 4.15 & 4.16), and are significantly different in mean values of upper and lower M3 length, width and crown height, lower M3 plate count and enamel thickness, and upper M3 lamellar frequency (Tables 4.11 & 4.12). Combined, this evidence supports the presence of two taxa in the Luparello Cave material, in line with Vaufrey's (1929) recognition of two stratigraphically separated, different-sized species from this site (Appendix A1.2.2) Unfortunately, no record is made of the stratigraphical provenance of individual specimens, preventing any test of stratigraphical-morphological relationships. However, 'Luparello 2' and 'Luparello 1' correspond, respectively, to the IPH labels' species designation of '*E. melitensis'* and *'E.' falconeri,* which may reflect Vaufrey's original stratigraphic delineation.

There is considerable overlap between Spinagallo Cave and Luparello 1 upper and lower M3 morphology (Figure 4.13 a&b). Lower and upper M3s from Spinagallo Cave form single clusters, with no evidence of bimodality, indicative of a single taxon at this site and in line with calculated CV values (single-species hypothesis not rejected, all variables, upper and lower M3s; Tables 4.13 & 4.14). However, the CV value for upper M3 lamellar frequency in a combined Spinagallo Cave-Luparello 1 (= 'Sicily 1') sample is significantly different from the highest full-sized comparator CV values, rejecting a single species hypothesis (Table 4.16; lower M3 length and crown height CV values are significantly higher than the second highest comparator, Table 4.15). Spinagallo Cave and Luparello 1 are also significantly different in plate count and enamel thickness (upper and lower M3s) and in upper M3 lamellar frequency (Tables 4.11 & 4.12).

These differences can be identified qualitatively in Figure 4.13 (a&b): Spinagallo Cave material tends to fall to the upper-right (lower right for LF) of the Sicily 1 cluster in these variables. Univariate box-plots (Figures 4.14 & 4.15) provide further evidence of consistent differences between Spinagallo Cave and Luparello 1: while Luparello Cave material is not split in these figures, Spinagallo Cave has larger median values of lower and upper M3 plate count, width and enamel thickness than the total Luparello Cave sample. Combined, this does not support the grouping of Luparello 1 and Spinagallo Cave into a single OTU (Sicily 1), despite considerable sample overlap. Overlap between these groups, however, makes taxonomic diagnosis problematic and I continue to investigate the implications of these groups as separate and combined OTUs.

Puntali Cave, Cavern (C.) di Carini and Za Minica overlap in upper and lower M3 morphology (Figure 4.13 d&e), although a lower M3 from C. di Carini, M5989, appears to be an outlier. CV values for these sites, individually or combined, cannot reject a single-species hypothesis (Tables 4.13 & 4.14; all variables, upper and lower M3s). Furthermore, mean values are not significantly different for any pair-wise comparisons between Za Minica and Puntali Cave dental variables (upper and lower M3), and for most comparisons between C. di Carini and Puntali Cave or Za Minica (Tables 4.11 & 4.12). Exceptions are (i) plate count (C. di Carini is significantly different from both in lower M3s,

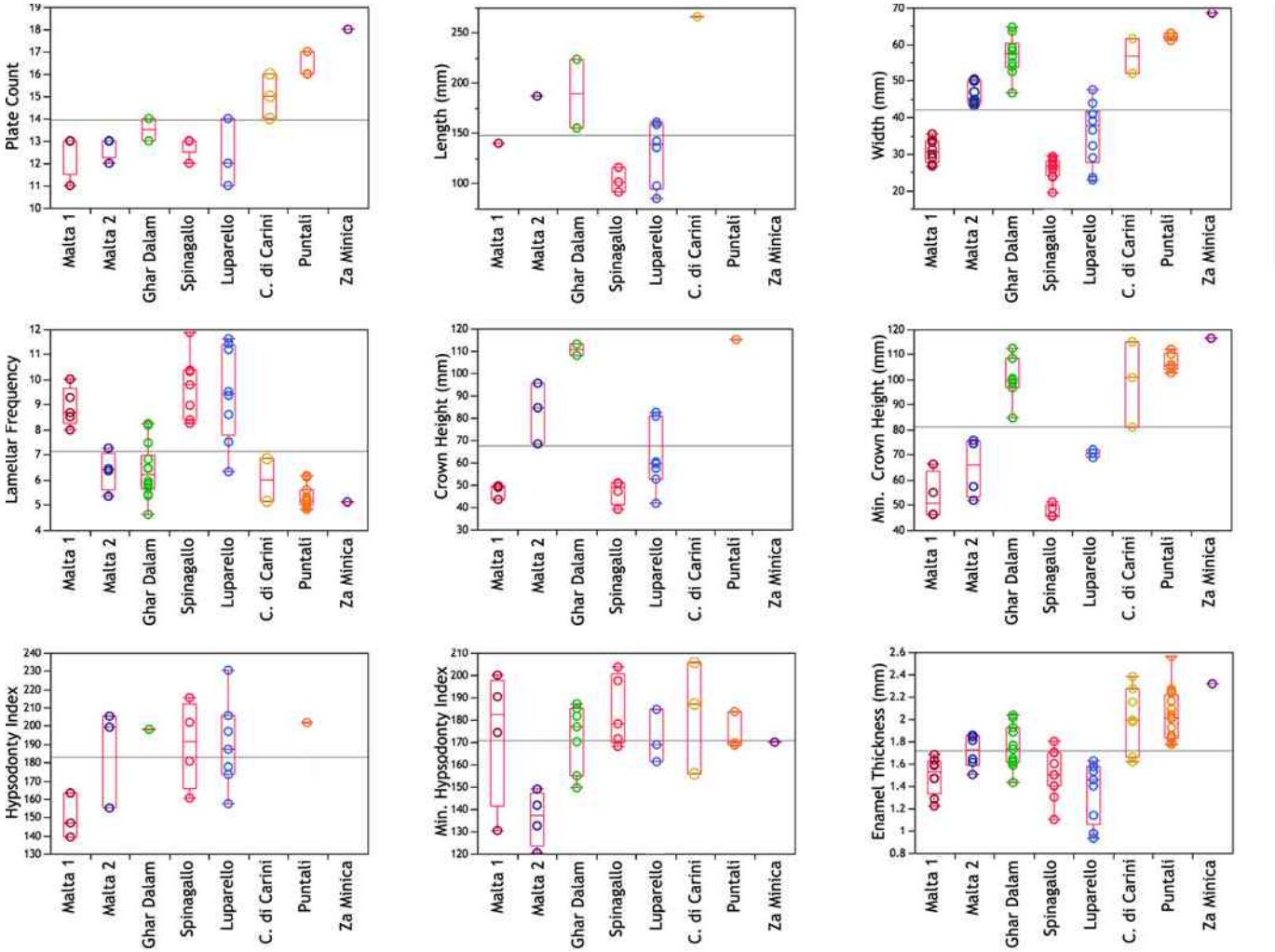

Figure 4.14. Box-plots of lower M3 variables for Maltese and Sicilian elephants. Malta 1 and Malta 2 are equivalent to the type-series for '*P. melitensis*' and *P. mnaidriensis*, respectively, and comprise molars from Mnadira Gap, Zebbug Cave, Gandia Fissure, Benghisa Gap and unknown localities in Malta. All other samples are grouped by fossil locality: Ghar Dalam, Malta and Spinagallo Cave, Luparello Cave, Cavern (C.) di Carini, Puntali Cave and Za Minica, Sicily. The Grand Mean (grey horizontal line) and site/OTU median (red horizontal line) are shown. The box, or interquartile range, is delineated by the upper 75% and lower 25% quartiles, and centred on the mean (not shown). The 'whiskers' extend to the outermost data-point contained within the calculated ranges = [75% quartile + 1.5 * (interquartile range)] and =[25% quartile – 1.5 * (interquartile range)].

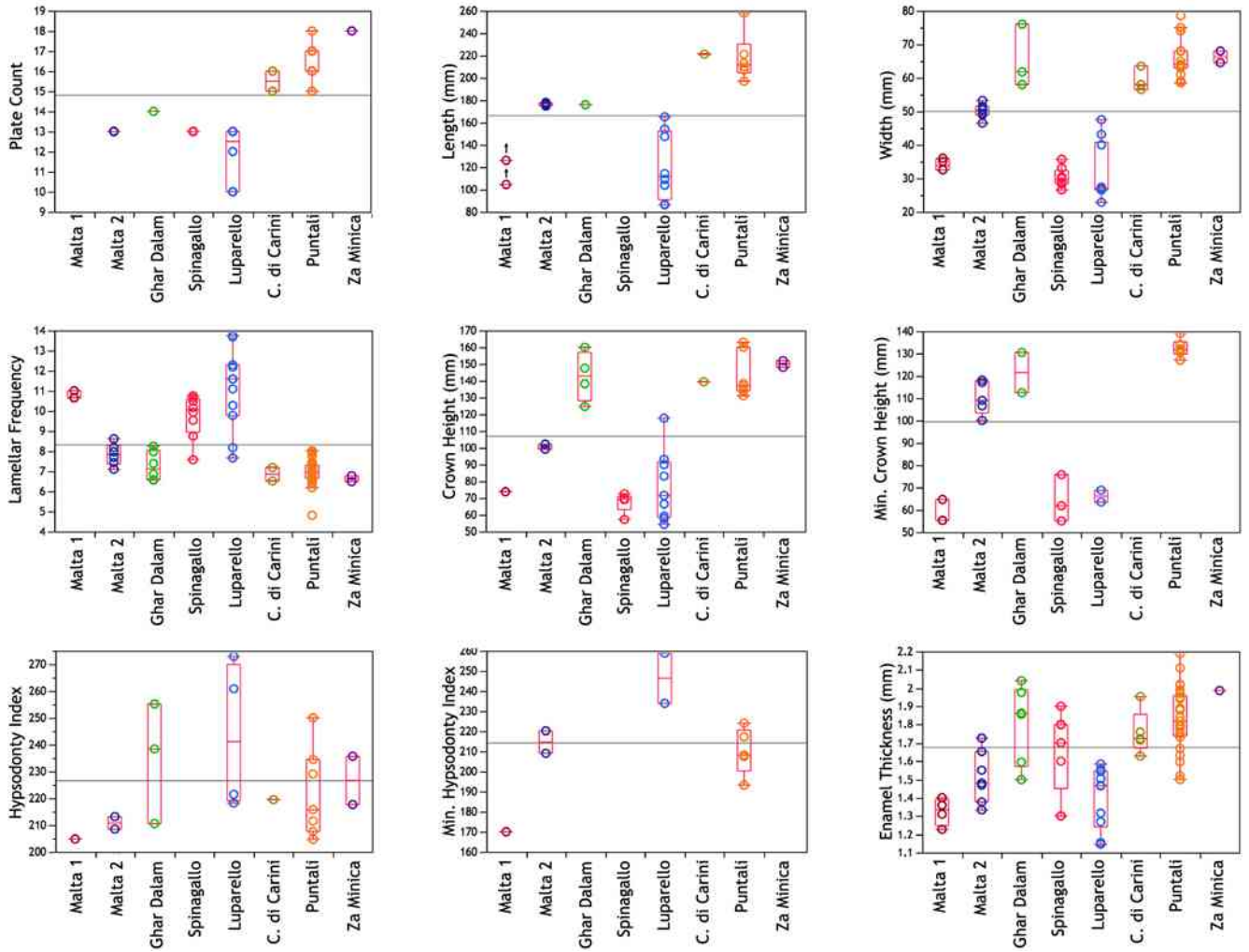

Figure 4.15. Box-plots of upper M3 variables for Maltese and Sicilian elephants. Figure legend and abbreviations as Fig 4.9. Malta 1 lengths are included for visual comparisons only; both have probably lost anterior root, and length measures are underestimates.

and from Za Minica in upper M3s) and (ii) upper M3 width (C. di Carini is significantly different from Za Minica). These three lines of evidence support the phenetic grouping of Puntali Cave, Za Minica and C. di Carini into a higher level OTU, referred to as 'Sicily 3'. However, it should be noted that, for pair-wise comparisons, non-significance could result from the low sample sizes of Za Minica and C. di Carini.

The larger Luparello mOTU (=Sicily 2) is delineated from both Luparello 1 and Spinagallo Cave material and from the large-sized Sicily 3. CV values for both a Sicily 2-Spinagallo Cave sample and a Sicily 1-Sicily 2 sample reject a single species hypothesis for lower M3 width and length and for upper M3 width and crown height (Tables 4.15 & 4.16). Mean values for Luparello 2 and Spinagallo Cave are also significantly different between upper and lower M3 width and crown height, and lower M3 length and minimum crown height (Tables 4.11 & 4.12; comparisons with Luparello 1 are described above). A combined Sicily 2-Sicily 3 sample rejects a single species hypothesis on the basis of lower M3 width and lamellar frequency (Table 4.15) and upper M3 crown height (Table 4.16). Luparello 2 is also significantly different in mean values for all possible pair-wise comparisons with each of the large-sized mOTUs, for all variables except hypsodonty indices, in upper and lower M3s (Tables 4.11 & 4.12). This confirms the hypothesized lack of conspecificity based on geochronological separation between material from these sites (Puntali Cave and Za Minica are younger than Luparello Cave; section 3.5.1).

C. di Carini, has an outlying lower M3 specimen (M5989) that is close in size to Luparello 2 material, and is the only site among the 'large' Sicily 3 specimens with no geochronological data. It was thus compared separately to Luparello 2 to confirm that phenetic delineation between these mOTUs was appropriate. The t-tests discussed above already suggest this is so, and CV values for a combined Sicily 2-C. di Carini sample reject a single-species hypothesis for lower M3 length, width, lamellar frequency and minimum crown height, and for upper M3 lamellar frequency and crown height (Tables 4.15 and 4.16). A taxonomic separation between these mOTUs is thus supported. However, the outlying C. di Carini specimen M5989 could be accommodated within the Sicily 2 sample without rejecting a single-species hypothesis (Table 4.15). This serves to underline the incremental nature and overlap of size differences between taxa, which, along with the added problem of allometric change explored below and in Chapter 6, make delineation of dwarf taxa within an island problematic.

Sicilian elephants can therefore be grouped into at least three OTUs on the basis of M3 morphology: a 'small-sized' dwarf (Sicily 1; although this grouping is less well supported), a 'medium-sized' dwarf (Sicily 2) and a 'large-sized' dwarf (Sicily 3), paralleling the three Maltese size-classes and grouping with their analogous Maltese size-class on the basis of molar width (Figures 4.16 & 4.17).

OTU	Plate Count					Length (mm)					Width (mm)					Lamellar Frequency					Crown Height (mm)					Min. Crown Height (mm)					Enamel Thickness (mm)				
	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV
Luparello 1	1	11.0	11	11	.	2	91.2	85.0	97.5	10.9	4	26.8	22.8	32.2	17.7	4	9.7	6.3	11.6	26.4	4	53.5	41.7	60.2	17.0	0	.	.	.	.	5	1.2	0.9	1.6	26.0
Sicily 1	6	12.5	11	13	6.7	4	98.5	85.0	116.0	14.5	15	26.2	19.3	32.2	12.4	11	9.7	6.3	11.9	17.4	8	50.2	39.1	60.2	15.5	8	50.2	39.1	60.2	5.5	15	1.4	0.9	1.8	19.8
Sicily 2	2	13.0	12	14	12.2	4	149.4	135.8	161.0	8.8	6	41.4	36.5	47.5	9.7	4	9.2	7.5	11.4	19.1	3	73.5	57.4	82.4	20.6	3	70.5	68.9	72.0	2.4	4	1.5	1.4	1.6	5.8
Sicily 3	10	16.1	14	18	7.0	1	266.0	266.0	266.0	.	8	61.6	52.0	68.5	7.6	18	5.4	4.8	6.9	10.4	1*	.	.	.	.	10	105.3	81.0	116.4	9.8	24	2.0	1.6	2.6	12.0
Sicily 1&2	8	12.6	11	14	7.5	8	123.9	85.0	161.0	24.7	21	30.5	19.3	47.5	25.8	15	9.6	6.3	11.9	17.1	11	56.6	39.1	82.4	25.4	8	56.0	45.5	72.0	22.4	19	1.4	0.9	1.8	17.6
Scily 1&3	16	14.8	11	18	14.1	6	126.2	85.0	266.0	57.2	24	38.1	19.3	68.5	46.0	30	7.0	4.8	11.9	33.8	9	57.4	39.1	115.0	40.7	16	84.5	45.5	116.4	34.9	41	1.8	0.9	2.6	22.0
Sicily 2 & SC	7	12.9	12	14	5.6	7	129.5	91.6	161.0	21.8	18	31.3	19.3	47.5	25.9	12	9.3	6.2	11.9	17.9	7	58.3	39.1	82.0	29.9	9	56.7	45.5	72.0	21.0	16	1.5	1.1	1.8	11.7
Sicily 2 & 3	9	15.8	12	18	11.6	4*	.	.	.	.	12	52.3	36.5	68.5	23.0	20	6.1	4.8	11.4	29.5	4	83.9	57.4	115.0	30.0	10	92.9	68.9	116.4	19.7	14	2.0	1.4	2.6	17.9
Sicily 2 & CC	5	14.2	12	16	11.0	5	172.7	135.8	266.0	32.4	8	45.3	36.5	61.5	18.7	6	8.1	5.1	11.4	27.7	3*	.	.	.	.	6	84.7	68.9	115.0	23.3	11	1.8	1.4	2.4	18.8
Sicily 2 & M5989	3	13.3	12	14	9.4	4*	.	.	.	.	7	43.0	36.5	52.0	12.8	5	8.7	6.9	11.4	21.4	3	.	.	.	.	4	73.1	68.9	81.0	7.8	5	1.5	1.4	1.7	6.4
Sicily 3 & L1	11	15.6	11	18	12.2	3	149.5	85.0	266.0	73.3	12	50.0	22.8	68.5	36.0	22	6.2	4.8	11.6	32.4	5	65.8	41.7	115.0	45.5	5	65.7	41.7	115.0	45.5	29	1.9	0.9	2.6	21.2
Sicily 3 & SC	15	12.0	12	18	12.6	4	143.7	91.6	266.0	60.7	20	40.4	19.3	68.5	45.5	26	6.6	4.8	11.9	32.0	5	60.5	39.1	115.0	53.5	16	84.5	45.5	116.4	34.9	36	1.9	1.1	2.6	18.1

Table 4.15. Summary Statistics of lower M3 dental measurements for putative Sicilian taxa. Legend as Table 4.13. * denotes a 'combined' sample that actually comprises just one of the constituent groups, and thus statistics are not repeated. Sicily 1 comprises Spinagallo Cave material and 'Luparello 1'. Sicily 2 is 'Luparello 2'. Sicily 3 comprises Puntali Cave, Za Minica and Cavern (C.) di Carini material. C. di Carini is also treated separately as it contains an outlier that causes overlap between taxon groups. SC is Spinagallo Cave and L1 is Luparello 1.

OTU	Plate Count					Length (mm)					Width (mm)					Lamellar Frequency					Crown Height (mm)					Min. Crown Height (mm)					Enamel Thickness (mm)				
	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV
Luparello 1	5	11.6	10	13	13.7	5	100.1	86.3	114.3	13.5	7	26.3	22.9	27.4	6.1	7	12.3	11.1	13.7	8.8	5	61.8	54.3	71.5	11.9	2	66.1	63.5	68.8	6.4	7	1.3	1.1	1.6	12.9
Sicily 1	9	12.2	10	13	10.9	5*	.	.	.	.	15	28.4	22.9	35.7	10.8	15	10.9	7.6	13.7	15.7	10	64.7	54.3	72.5	10.8	5	65.0	55.0	75.8	12.6	16	1.5	1.1	1.9	16.7
Sicily 2	1	13.0	13	13	.	3	155.5	147.5	165.0	6.2	3	43.6	40.0	47.5	9.4	4	9.0	7.7	10.3	14.8	4	96.0	83.1	117.7	16.7	0	.	.	.	.	3	1.5	1.5	1.6	4.3
Sicily 3	20	16.5	15	18	5.4	7	218.2	197.0	257.9	9.2	24	64.9	56.5	78.5	8.4	29	6.9	4.8	8.0	9.2	10	143.8	131.0	163.0	7.8	6*	.	.	.	.	31	1.8	1.5	2.2	9.1
Sicily 1&2	10	12.3	10	13	10.4	8	120.9	86.3	165.0	26.2	18	30.9	22.9	47.5	21.6	19	10.5	7.6	13.7	17.1	14	73.6	54.3	117.7	23.9	5*	.	.	.	.	19	1.5	1.1	1.9	15.2
Sicily 1 & 3	29	15.1	10	18	14.7	12	169.0	86.3	257.9	32.8	39	50.9	22.9	78.5	36.8	44	8.3	4.8	13.7	26.8	20	104.2	54.3	163.0	40.4	11	101.7	55.0	139.0	35.8	47	1.7	1.1	2.2	14.3
Sicily 2 & SC	5	13.0	13	13	0.0	3	.	.	.	.	11	33.8	26.6	47.5	20.9	12	9.5	7.6	10.8	12.4	9	80.2	57.3	117.7	23.2	3	.	.	.	.	12	1.6	1.3	1.9	12.3
Sicily 2 & 3	19	16.4	13	18	7.2	9	196.9	147.4	257.9	18.6	24	62.9	40.0	78.5	14.4	31	7.2	4.8	10.3	14.1	13	129.4	83.1	163.0	20.7	6*	.	.	.	.	29	1.8	1.5	2.2	10.5
Sicily 2 & CC	3	14.7	13	16	11.3	4	171.9	147.4	221.2	20.8	6	51.4	40.0	63.5	18.8	6	8.3	6.5	10.3	18.6	5	104.6	83.1	139.4	23.5	0	.	.	.	.	8	1.7	1.5	2.0	9.3
Sicily 3 & SC	24	15.9	13	18	9.8	7	.	.	.	.	32	56.2	26.6	78.5	28.7	37	7.5	4.8	10.8	18.5	15	118.4	57.3	163.0	33.0	9	109.6	55.0	139.0	32.5	40	1.8	1.3	2.2	10.7
Sicily 3 & L1	25	15.5	10	18	14.5	12	169.0	86.2	257.9	38.0	31	56.2	22.9	78.5	30.7	36	8.0	4.8	13.7	28.8	15	116.5	54.3	163.0	35.9	8	115.8	63.5	139.0	27.5	38	1.7	1.1	2.2	14.5

Table 4.16. Summary Statistics of upper M3 dental measurements for putative Sicilian taxa. Legend as Table 4.15.

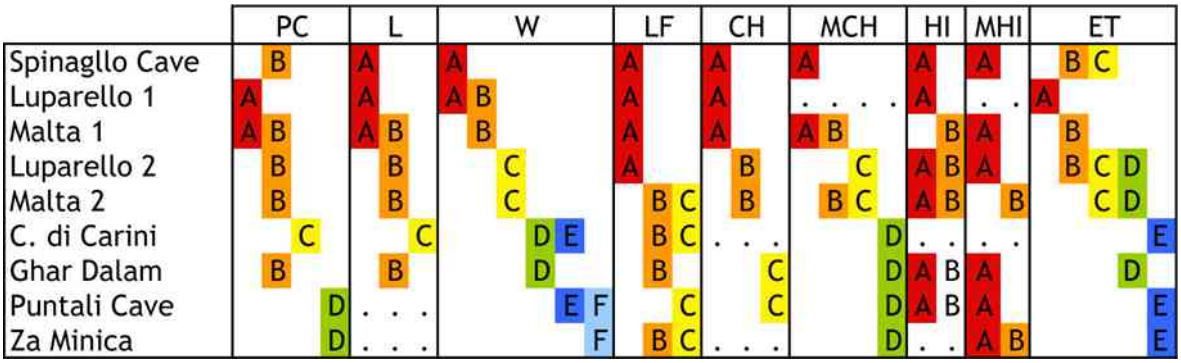

Figure 4.16. Significant differences in lower M3 parameters of Maltese and Sicilian dwarf elephant mOTUs. Summary of data from Table 4.11; mOTUs connected by the same letter/colour are not significantly different for that parameter. PC is plate count, L is length (mm), W is width (mm), LF is lamellar frequency, CH is crown height (mm), MCH is minimum crown height, HI is hypsodonty index, MHI is minimum hypsodonty index. ET is enamel thickness.

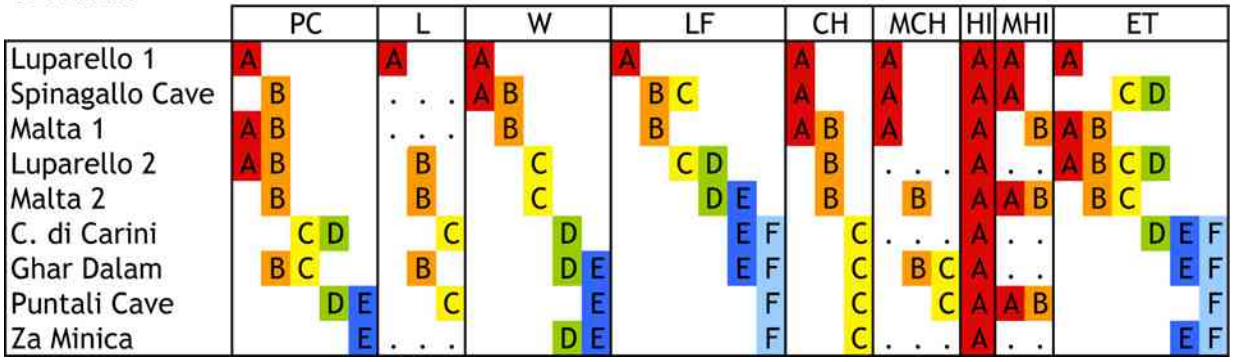

Figure 4.17. Significant differences in upper M3 parameters of Maltese and Sicilian dwarf elephant mOTUs. Summary of data from Table 4.12; Legend as Figure 4.16.

Comparing Sicilian and Maltese mOTUs

There is considerable overlap between Malta 1 and Spinagallo and Luparello Caves in all univariate dental variables (Figures 4.14 & 4.15). CV values for a combined Malta 1-Sicily 1 cannot reject a single species hypothesis (all variables, upper and lower M3s; Tables 4.17 & 4.18), although lower M3 length, width and crown height are all significantly higher than the second-highest full-sized comparator value. However, Sicily 1 has been shown to be incompatible with a single species hypothesis and when 'small-sized' Sicilian mOTUs are compared with Malta 1 separately, CV values cannot reject a single species hypothesis for Malta 1 and Spinagallo Cave (all variables, upper and lower M3s. Tables 4.17 & 4.18) but can for Malta 1 and Luparello 1 (lower M3 length; Table 4.17).

Pair-wise comparisons of mean values, however, show a significant difference between Malta 1 and Spinagallo Cave in lower M3 width and hypsodonty index (HI) (Malta 1 has wider, lower crowned molars; Table 4.11, Figure 4.16) and upper M3 enamel thickness (Spinagallo Cave has thicker enamel; Table 4.12, Figure 4.17. This difference is amplified when relative enamel thickness is considered – see below). Malta 1 and Luparello Cave are also significantly different in mean values of lower M3 HI and enamel thickness (Malta 1 is again lower crowned, but this time has thicker enamel; Table 4.11, Figure 4.16) and in upper M3 width, lamellar frequency and minimum HI (Malta 1 is wider, relatively lower crowned and has a lower lamellar frequency; Table 4.12, Figure 4.16). The difference in HI between Malta 1 and the Sicilian mOTUs appears to be driven by the greater width of Malta 1 M3s (even if this measure in non-significant in some comparisons): Malta 1, Spinagallo Cave and the smaller Luparello specimens overlap in crown height and minimum crown height but their HIs are divergent (Figures 4.14 & 4.15). However, sample sizes for this index are very low (complete or near complete crown heights are rare due to wear) and the true range of variation is not sampled in Malta 1 (min. HI values exceed HI values in lower M3s, Figure 4.14).

Malta 1 upper M3 length is not included in quantitative comparisons as the two most complete specimens (plotted in Figure 4.15) have lost their anterior root section to wear, and their lengths are significant underestimates. However, it is clear that these specimens would exceed Luparello 1 material in length (Figure 4.15; Figure 4.7 also pictures an incomplete Spinagallo Cave upper M3 alongside NHM 44312 – the shorter of the two Malta 1 M3s - for comparison). Lower M3 length is also greater in Malta 1 (Figure 4.14); although mean differences are not significant (Table 4.11, Figure 4.16) this is likely due to low sample size of Mata 1 (n=1).

On bivariate plots, Malta 1 lower M3s fall to the right of both Spinagallo Cave and Luparello 1 specimens (i.e. are wider), but the 95% confidence ellipses for these groups overlap considerably or encompass each other (Figure 4.18). However, Malta 1 often falls outside of, or overlaps only slightly with, the 95% confidence ellipses for Sicily 1 upper M3s, further illustrating width differences between these mOTUs (Figure 4.19). Malta 1 also either overlaps of falls within the 95% confidence ellipses of Luparello 2, while there is clear delineation between Luparello 2, Luparello 1 and Sicily 1 (Figures 4.18 & 4.19).

OTU	Plate Count					Length (mm)					Width (mm)					Lamellar Frequency					Crown Height (mm)					Min. Crown Height (mm)					Enamel Thickness (mm)				
	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV
M1 & S1	10	12.5	11	13	7.0	6	105.2	85.0	140.0	19.8	23	27.8	19.3	35.4	13.9	16	9.4	6.3	11.9	15.7	11	49.4	39.1	60.2	13.7	9	50.0	45.5	66.2	14.1	25	1.4	0.9	1.8	16.6
M1 & SC	9	12.7	11	13	5.7	4	112.2	91.6	140.0	19.9	20	28.0	19.3	35.4	13.4	13	9.1	6.2	11.9	15.6	7	47.1	39.1	50.9	9.6	10	51.2	45.5	66.2	15.1	21	1.5	1.1	1.8	12.4
M1 & L1	5	12.2	11	13	9.4	3	107.5	85.0	140.0	29.1	12	29.4	22.8	35.4	13.7	9	9.2	6.3	11.6	18.0	7	50.8	41.7	60.2	14.6	4	.	.	.	.	14	1.4	0.9	1.7	18.2
M1 & S2	6	12.7	11	14	8.5	5	147.5	135.8	161.0	8.2	14	35.3	26.6	47.5	18.5	9	9.0	7.5	11.4	13.2	6	60.4	43.4	82.4	29.4	7	60.7	46.1	72.0	19.4	13	1.5	1.2	1.7	10.2
M1 & S3	11	15.1	11	18	14.9	1	.	.	.	.	14	44.7	26.6	68.5	38.6	21	6.2	4.8	10.0	27.0	4	64.2	43.4	115.0	56.3	11	88.2	46.1	116.4	32.8	26	1.8	1.2	2.6	19.2
M2 & S1	10	12.6	11	13	5.7	6	113.1	85.0	186.9	34.7	23	32.3	19.3	50.5	30.1	16	8.6	5.4	11.9	25.0	11	59.1	39.1	95.5	30.4	10	55.8	45.5	75.8	21.1	23	1.5	0.9	1.9	17.9
M2 & SC	9	12.8	12	13	3.5	4	124.0	91.6	186.9	37.0	19	33.4	19.3	50.5	30.6	12	8.3	5.4	11.9	24.9	7	62.3	39.1	95.5	35.1	10*	.	.	.	.	18	1.6	1.1	1.9	12.7
M2 & L1	5	12.4	11	13	7.6	3	123.1	85.0	186.9	48.9	11	38.8	22.8	50.5	26.7	8	8.0	5.4	11.6	31.2	7	66.0	41.7	95.5	29.1	4	.	.	.	.	11	1.5	0.9	1.9	22.9
M2 & S2	6	12.8	12	14	6.1	5	156.9	135.8	186.8	13.3	13	43.7	36.5	50.5	9.5	8	7.8	5.4	11.4	25.8	6	78.1	57.4	95.5	17.8	7	67.3	51.8	75.8	14.0	10	1.6	1.4	1.9	9.6
M2 & S3	11	15.2	12	18	13.7	1	.	.	.	.	15	54.2	42.4	68.5	17.1	20	5.5	4.8	7.3	12.1	4	90.8	68.3	115.0	23.0	11	92.4	51.8	116.4	25.6	23	2.0	1.5	2.6	13.2
GD & S1	8	12.8	11	14	7.2	7	124.3	85.0	223.5	41.3	26	38.1	19.3	64.6	41.5	26	7.8	4.6	11.9	27.7	10	62.3	39.1	113.0	43.3	13	76.9	45.5	112.4	36.0	28	1.6	0.9	2.0	18.3
GD & S2	4	13.3	12	14	7.7	6	162.7	135.8	223.5	20.1	16	51.1	36.5	64.6	17.9	18	7.0	4.6	11.4	24.5	5	88.3	57.4	113.0	26.9	10	91.3	68.9	112.4	18.0	15	1.7	1.4	2.0	11.9
GD & S3	9	15.9	13	18	9.9	2	.	.	.	.	16	59.3	46.6	68.5	9.3	30	5.8	4.6	8.2	16.2	3	112.0	108.0	115.0	3.5	14	104.1	84.7	116.4	7.8	28	1.9	1.4	2.6	13.5
M2, S3, GD	13	14.9	12	18	13.5	3	.	.	.	.	23	55.3	42.4	68.5	14.5	34	5.9	4.6	8.2	15.9	6	97.4	68.3	115.0	19.6	18	95.4	51.8	116.4	20.1	34	1.9	1.4	2.6	13.6
M2, S2, S3, GD	18	14.7	12	18	12.7	8	178.6	135.8	266.0	26.0	31	52.7	36.5	68.5	17.3	40	6.2	4.6	11.4	23.0	9	89.4	57.4	115.0	23.0	24	92.7	51.8	116.4	20.8	45	1.9	1.4	2.6	14.7

Table 4.17. Summary statistics of lower M3 dental measurements for combined Maltese and Sicilian OTUs. Legend as Table 4.15.

OTU	Plate Count					Length (mm)					Width (mm)					Lamellar Frequency					Crown Height (mm)					Min. Crown Height (mm)					Enamel Thickness (mm)				
	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV	n	Mean	Min	Max	CV
M1 & S1	10	12.3	10	13	10.4	5*	.	.	.	.	19	29.6	22.9	36.0	12.5	18	10.9	7.6	13.7	14.2	11	65.5	54.3	73.8	10.7	8	62.5	55.0	75.8	12.2	20	1.5	1.1	1.9	16.2
M1 & SC	5	13.0	13	13	0	1	.	.	.	.	11	31.4	26.6	36.0	10.7	10	9.9	7.6	11.0	11.0	6	68.6	57.3	73.8	8.9	5	62.5	55.0	75.8	14.3	12	1.6	1.2	1.9	16.0
M1 & L1	6	11.8	10	13	13.0	6*	.	.	.	.	10	28.8	22.9	36.0	15.2	9	12.0	10.7	13.7	9.6	6	63.8	54.3	73.8	12.9	4	63.1	55.3	688.0	9.5	10	1.3	1.1	1.6	11.0
M1 & S2	2	13.0	13	13	0.0	4	142.7	104.5	165.0	19.7	6	39.0	32.5	47.5	14.9	6	9.6	7.7	11.0	14.9	5	91.5	73.8	117.7	18.8	2	60.0	1.0 55.3	64.7	12.4	6	1.4	1.2	1.6	10.0
M1 & S3	19	16.6	13	18	7.2	6*	.	.	.	.	24	61.8	32.5	78.5	19.0	29	7.2	4.8	11.0	16.6	10	137.2	73.8	163.0	18.6	8	114.3	55.3	139.0	30.5	29	1.8	1.2	2.2	13.1
M2 & S1	14	12.5	10	13	8.9	10	138.3	86.3	178.0	30.5	24	36.1	22.9	53.3	29.7	23	9.9	7.1	13.7	19.8	12	70.7	54.3	102.2	22.1	10	87.6	55.0	118.1	29.1	25	1.5	1.1	1.9	14.0
M2 & SC	9	13.0	13	13	0.0	5	.	.	.	.	17	40.1	26.6	53.3	25.6	16	8.9	7.1	10.8	14.1	7	77.0	57.3	102.2	22.7	8	92.9	55.0	118.1	27.9	18	1.6	1.3	1.9	11.8
M2 & L1	10	12.3	10	13	10.4	10*	.	.	.	.	16	39.1	22.9	53.3	30.9	15	10.1	7.1	13.7	23.7	7	72.9	54.3	102.2	28.1	7	97.6	63.5	118.1	23.8	16	1.4	1.1	1.7	12.0
M2 & S2	6	13.0	13	13	0.0	8	168.6	147.4	178.0	7.3	12	47.6	40.0	53.3	8.7	12	8.4	7.1	10.3	11.9	6	97.5	83.1	117.7	12.8	5*	.	.	.	.	12	1.5	1.3	1.7	7.4
M2 & S3	23	15.8	13	18	10.7	11	198.9	174.7	257.9	13.5	30	60.7	42.2	78.5	15.1	35	7.2	4.8	9.4	11.5	11	136.4	99.1	163.0	15.5	11	122.3	100.0	139.0	10.7	35	1.8	1.3	2.2	12.0
GD & S1	10	12.4	10	14	11.2	6	112.7	86.4	176.0	30.6	18	34.5	22.9	76.0	43.4	21	9.9	6.6	13.7	22.9	14	86.9	54.3	160.0	44.1	7	81.1	55.0	130.5	36.3	22	1.6	1.1	2.0	17.0
GD & S2	2	13.5	13	14	5.9	4	160.6	147.4	176.0	8.3	6	54.4	40.0	76.0	25.9	10	7.9	6.6	10.3	16.2	8	119.3	83.1	160.0	24.7	2*	.	.	.	.	9	1.7	1.5	2.0	13.2
GD & S3	19	16.4	14	18	6.3	7	211.7	176.0	257.9	11.8	24	65.7	58.0	78.5	8.6	33	7.0	4.8	8.2	9.6	13	143.8	124.7	163.0	8.6	8	129.6	112.5	139.0	6.1	32	1.8	1.5	2.2	9.7
M2, S3, GD	24	15.7	13	18	10.7	12	197.0	174.7	257.9	13.4	33	61.1	42.2	78.5	15.0	41	7.2	4.8	9.4	11.2	15	138.0	99.1	163.0	14.0	13	122.1	100.0	139.0	10.3	41	1.8	1.3	2.2	11.9
M2, S2, S3, GD	25	15.6	13	18	11.2	15	188.7	147.4	257.9	15.6	36	59.6	40.0	78.5	16.9	45	7.4	4.8	10.3	13.3	19	129.7	83.1	163.0	19.7	13	122.1	100.0	139.0	10.3	44	1.8	1.3	2.2	12.1

Table 4.18. Summary statistics of upper M3 dental measurements for combined Maltese and Sicilian OTUs. Legend as Table 4.15.

The phenetic grouping of Malta 1, Luparello 1 and Spinagallo Cave into a higher level OTU is therefore supported by CV-based single-species hypothesis testing, but significant differences between all groups for key mean dental variables weaken this grouping. The rejection of a single species hypothesis for Luparello 1 with Malta 1, and for Luparello 1 with Sicily 1 also suggests that Luparello 1 should be excluded from a putative phenetic grouping of Malta and Sicily 1.

Malta 1 and Malta 2 are clearly delineated from one another, but both show overlap, (in range or in 95% confidence ellipses), with Luparello 2 (Figures 4.18 & 4.19). A combined Malta 1-Luparello 2 sample rejects a single species hypothesis for one variable, lower M3 width, although upper and lower M3 crown height are also rejected by the second-highest full-sized comparator CV (Table 4.17 & 4.18). Malta 1 and Luparello 2 are also significantly different in lower M3 mean width, crown height and minimum crown height and in upper M3 width and lamellar frequency (Tables 4.11 & 4.12). Combining Malta 1 and Luparello 2 into a higher level OTU is therefore not supported.

A combined Malta 2-Luparello 2 sample cannot reject a single species hypothesis (all variables, upper and lower M3s), although lower M3 length, lamellar frequency and crown height reject a single-species hypothesis based on the second highest full-sized comparator CV (Table 4.17). Malta 2 and Luparello 2 are significantly different in mean value of lower M3 width, lamellar frequency and minimum crown height (Table 4.11); all upper M3 pairwise comparisons are non-significant. Consequently, despite the overlap between Malta 1 and Luparello 2, the combined evidence supports the grouping of Luparello 2 and Malta 2 to the exclusion of Malta 1.

Malta 2 is significantly different from Puntali Cave, Za Minica and C. di Carini material for all variables except (i) HIs (which do not differentiate between any palaeoloxodontine-type molar – see below), and, for C. di Carini only, (ii) upper M3 lamellar frequency (upper and lower M3s; Tables 4.11 & 4.12). However, both Ghar Dalam and C. di Carini overlap with Malta 2, or with the 95% confidence ellipses of Malta 2, and with Puntali Cave and Za Minica, illustrating the incremental nature of overlap between dwarf mOTUs (Figure 4.18 & 4.19). CV evidence rejects a single-species hypothesis for a combined Sicily 3-Malta 2 sample on lower M3 width; and lower M3 crown height and upper M3 width and crown height reject a single species based on comparisons with the second highest full-sized comparator (Tables 4.17 & 4.18).

A combined Ghar Dalam-Sicily 3 sample cannot reject a single-species hypothesis for any variable. However, Ghar Dalam is significantly different from Puntali Cave in mean plate count (upper and lower M3s), mean length (upper M3s) and mean width, lamellar frequency and enamel thickness (lower M3s); from Za Minica in mean plate count (upper and lower M3s), and mean width and enamel thickness (lower Ms); and from C. di Carini in mean length (upper and lower M3s), and mean plate count and enamel thickness (lower M3s) (Tables 4.11 & 4.12). Thus despite overlap and sample variation compatible with a single-species hypothesis there is clear ‘structure’ within a putative taxonomic grouping of Ghar Dalam and Sicily 3.

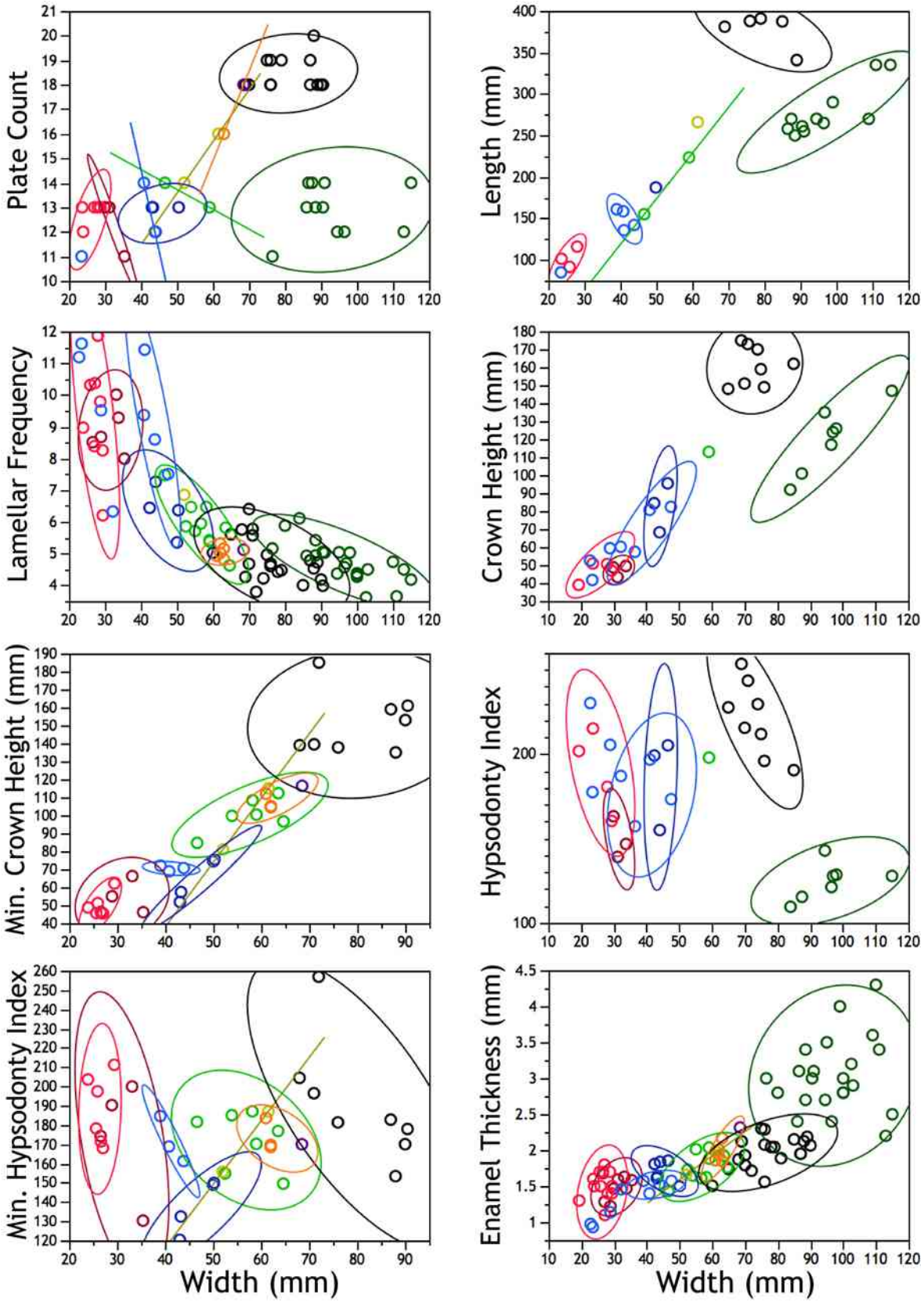

Figure 4.18. Bivariate scatter plots for Sicilian and Maltese dwarf elephants and *P. antiquus* and *M. meridionalis* Lower M3 with 95% confidence ellipses for putative taxa. Points: light red, Spinagallo Cave; light blue, Luparello Cave; dark red, Malta 1; dark blue, Malta 2; light green, Ghar Dalam; yellow, C. di Carini; orange, Puntali Cave; purple, Za Minica; black, *P. antiquus*; dark green, *M.meridionalis*. 95% confidence ellipses follow point colours, except light red is Sicily 1 and light blue is Sicily 2.

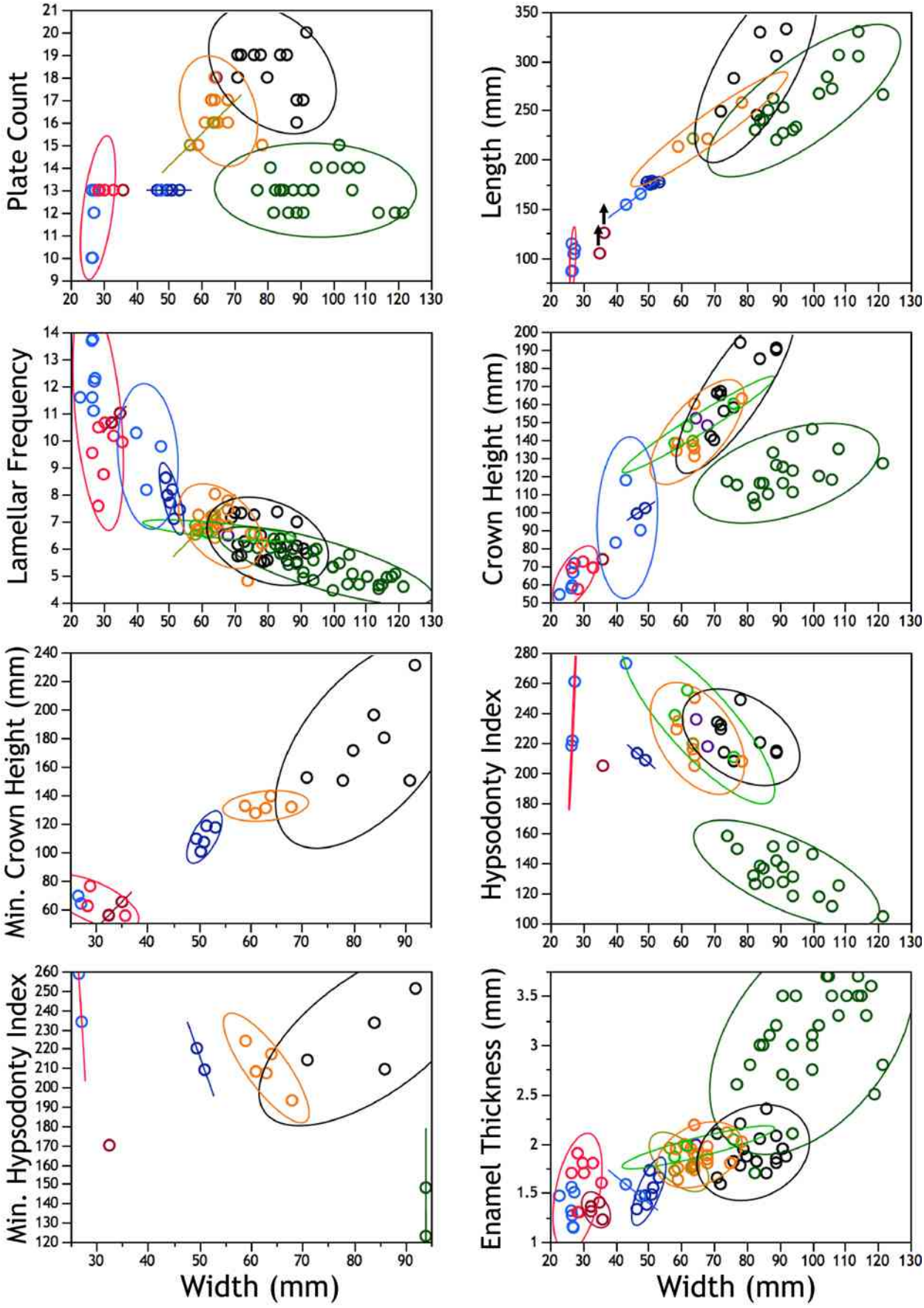

Figure 4.19. Bivariate scatter plots for Sicilian and Maltese dwarf elephants and *P. antiquus* and *M. meridionalis* Upper M3 with 95% confidence ellipses for putative taxa. Point and 95% ellipse colours as in Figure 5.17.

A combined Malta 2-Ghar Dalam-Sicily 3 sample cannot, however, reject a single species hypothesis for any variable based on CV (although lower M3 width and crown height, and upper M3 width do so based on the second highest full-size comparator). This creates a further dilemma: a combined Malta 2-Luparello 2 sample also cannot reject a single species hypothesis, thus a phenetic group of Malta 2, Ghar Dalam and Sicily 3 must also include Luparello 2. When Luparello 2 is included, however, CV values reject a single species hypothesis for lower M3 length, width and lamellar frequency (Table 4.17) and upper M3 crown height (Table 4.18). A combined sample of Ghar Dalam-Luparello 2 also rejects a single species hypothesis on the basis of lower M3 width and lamellar frequency, and upper M3 crown height CV values (Tables 4.17 & 4.18), as well as being significantly different from each other in upper and lower M3 width, lamellar frequency, crown height and enamel thickness, lower M3 minimum crown height and upper M3 length (Tables 4.15 & 4.16). Given the evidence against (i) a Malta 2-Ghar Dalam phenetic grouping (Table 4.13), (ii) Luparello 2-Ghar Dalam grouping, (iii) a Sicily 3-Malta 2 grouping, and (iv) evidence for a possible phenetic grouping of Luparello 2 with Malta 2, I advocate the taxonomic delineation of Malta 2 from Sicily 3 based on dental variables.

Diagnosing Sicilian and Maltese taxa using molar morphology

The incremental nature of size differences between dwarf taxa leads to overlap between many mOTUs at either extreme of their ranges, for many molar variables (Figures 4.16-4.19). This inhibits species delineation: while two mOTUs may be significantly different in mean value, and incompatible with a single species hypothesis, for a number of variables, each may not reject conspecifity with an mOTU of intermediate size. The ability to diagnose a species (i.e. identify an individual specimen to species level on the basis of its morphological characteristics) provides further insight into the taxonomy of Maltese and Sicilian elephants (Figure 4.20).

Despite the evidence for multiple taxa within the 'small' size-class, it is not possible to diagnose individual mOTUs on the basis of dental parameters, although Malta 1 appears to have much longer M3s and Spinagallo Cave to have lower lamellar frequencies in upper M3s (Figure 4.20; as there are no complete lengths for Spinagallo Cave, the validity of this character as a diagnostic tool remains unknown), and hence they are here conservatively treated as a single-species. Malta 2 and Luparello 2 (=Sicily 2), the medium-sized taxa, cannot be diagnosed from one another (Figure 4.20). Ghar Dalam and Sicily 3, despite being broadly undiagnosable and – when combined - compatible with a single species hypothesis, show a number of significant differences in dental variables, most notably in plate count, that provide evidence against the phenetic grouping of these mOTUs (Figure 4.20). If Ghar Dalam is ignored (because of the highly-rolled nature of the material, and the suggestion it may not represent a single taxon), 'large-' and 'medium-sized' mOTUs both reject a single species hypothesis when combined, and can be diagnosed on the basis of all variables except lamellar frequency (Figure 4.20).

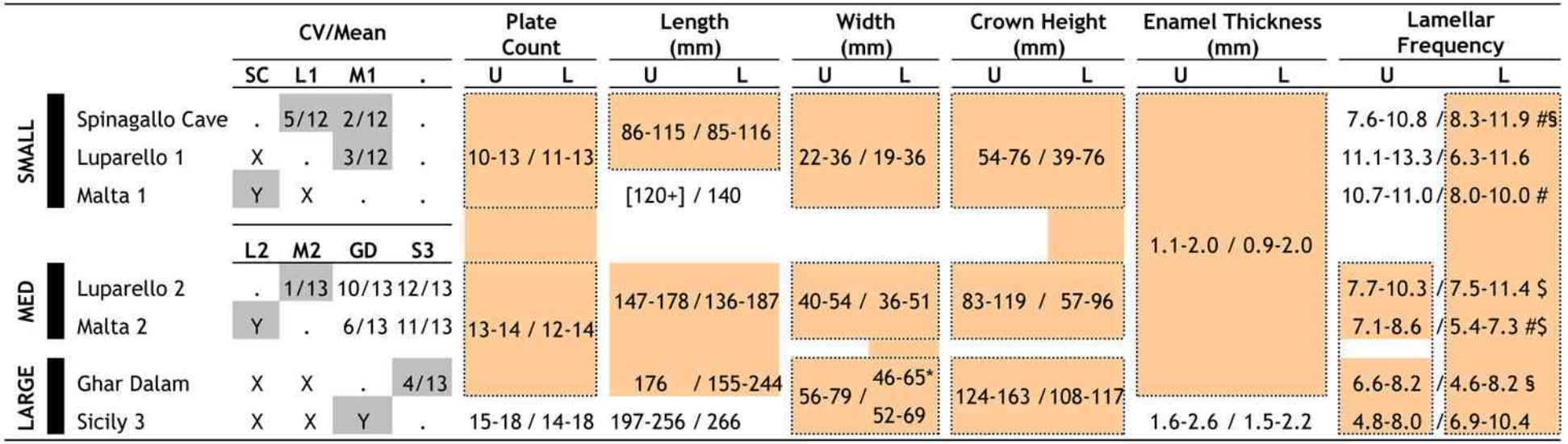

Figure 4.20. Diagnosing Sicilian and Maltese taxa. Sicilian and Maltese mOTUs can be grouped (black bars) into 'small', 'medium' (MED) and 'large' size-classes. CV/Mean summarises the evidence for a single species hypothesis within each size-class: below the diagonal, a single species hypothesis for the mOTU pair is supported (Y) or rejected (X) by CV evidence; above the diagonal, the number of significant t-test comparisons between mOTUs is expressed as a fraction of the total possible comparisons for each pair. Good support (grey shading) for a single-species hypothesis is provided if CV = Y and less than 50% of parameter means are significantly different (50% is n arbitrary cut-off, but indicates that mOTUs are not significantly different for the majority of parameters). Dental parameter ranges are summarised for upper and lower M3s. mOTUs with similar ranges are grouped within a dotted-box; orange shading groups overlapping ranges. * Ghar Dalam molar width of 46mm is an outlier, the next highest width is 52mm. SC is Spinagallo Cave, L1 is Luparello 1, M1 is Malta 1, L2 is Luparello 2, M2 is Malta 2, GD is Ghar Dalam and S3 is Sicily 3. **#**, **$** and **§** link mOTUs that do not overlap in lower lamellar frequency; the incremental overlap between mOTUs and the large ranges in this parameter make it difficult to clearly delineate mOTUs for this measure.

Taking 'diagnosability' as a conservative approach to taxonomic revision, and recognising the presence of phenetic 'structure' within these taxonomic groupings that might indicate evolutionary differences, this supports the grouping of Maltese and Sicilian elephants into three differently sized taxa: small (Spinagallo Cave, Luparello 1 and Malta 1), medium (Luparello 2 and Malta 2) and large (Sicily 3). Ghar Dalam remains problematic. In consequence, and without recourse to the consideration of contextual data, the evidence from phenetic grouping of dental material is at odds with the current two-species taxonomy for Sicily and Malta.

Crete

CV values for *M. creticus* (Bate 1907) lower molars cannot reject a single species hypothesis (Table 4.19; there are two *M. creticus* upper molar specimens, but these are fragmentary and not included in this study). The small sample size precludes a meaningful visual assessment of phenetic clustering, but *M. creticus* material falls outside of the *P. antiquus* CRETE range and CV values for a combined Cretan sample rejects a single species hypothesis for lower M3 width, crown height and minimum crown height (Figure 4.21a, Table 4.19). Cape Maleka material is thus consistent with a single species hypothesis, and the validity of *M. creticus* is supported.

The two large-sized *P. antiquus* CRETE specimens were excavated from East Crete. The larger tooth, NHMH 20.1.33, was misidentified by Poulakakis *et al.* (2002a) as an almost complete, right upper M2. It is actually an incomplete left, lower M3 (Figure 4.9). This specimen is considerably larger than NHM M9384 (Figure 4.9), although CV values cannot reject a single species hypothesis for width, possibly due to the small sample size. A single-species hypothesis is also rejected for enamel thickness (Table 4.19). M9384 may not be an M3: only the anterior portion of the molar is present, and although a curved morphology and narrowing posterior plates suggest M3 attribution, this is not certain as the tooth is partially encased in jaw bone. These data alone cannot be used as evidence for the presence of multiple large-sized elephant taxa on Crete, and needs to be assessed in light of more large-sized material from Crete to properly identify its place in the molar series. NHMH 20.1.33 is attributed to *P. a. creutzburgi* by Poulakakis *et al.* (2002a), and the authors suggest that the tooth is not sufficiently different in size to mainland *P. antiquus* to merit full specific delineation. This specimen is similar in molar width and height to C. di Carini material (Figure 4.31), and falls outside of the *P. antiquus* range. However, as with the above taxonomic issues, more material is required to assess the validity of *P. creutzburgi* as a species or a sub-species, and *P. antiquus* CRETE is retained here pending further investigation.

Cyprus

CV values for *P. cypriotes* upper and lower M3s cannot reject a single-species hypothesis (Tables 4.19 & 4.20), and there is no evidence of distinct clusters of M3s or the suggestion of multiple 'developmental' (dP4-M3) trajectories (Figure 4.21b&c). A lower M3, M8592, appears to be

	Plate Count					Length (mm)					Width (mm)					Lamellar Frequency					Crown Height (mm)					Min. Crown Height (mm)					Enamel Thickness (mm)				
Species	**n**	**Mean**	**Min**	**Max**	**CV**	**n**	**Mean**	**Min**	**Max**	**CV**	**n**	**Mean**	**Min**	**Max**	**CV**	**n**	**Mean**	**Min**	**Max**	**CV**	**n**	**Mean**	**Min**	**Max**	**CV**	**n**	**Mean**	**Min**	**Max**	**CV**	**n**	**Mean**	**Min**	**Max**	**CV**
P. cypriotes	2	11.5	11	12	6.9	3	111.4	93.6	127.3	16.5	4	28.9	24.3	33.4	13.8	2	9.6	9.6	9.7	1.3	1	59.7	59.7	59.7	.	2	46.3	39.9	52.6	21.9	4	1.2	1.1	1.3	7.7
M. creticus	2	12.0	12	12	0.0	1	144.0	144.0	144.0	.	3	37.1	33.4	40.7	10.7	3	9.4	8.3	11.4	19.4	2	44.2	38.9	49.6	19.2	1	27.8	27.8	27.8	.	2	1.9	1.9	1.9	1.7
P. antiquus Crete	0	.	.	.	.	0	.	.	.	.	2	54.8	47.6	62.0	20.9	2	6.8	7.2	7.2	9.5	1	97.0	97.0	97.0	.	1	97.7	97.7	97.7	.	2	1.7	1.3	2.1	37.8
All Crete	2*	.	.	.	.	0	.	.	.	.	5	44.2	33.4	62.0	26.7	5	8.4	6.4	11.4	23.6	3	61.8	38.9	97.0	54.2	2	62.7	27.8	97.7	88.7	4	1.8	1.3	2.1	20.9
P. tiliensis	1	13.0	13	13	.	0	.	.	.	.	1	49.2	49.2	49.2	.	1	6.1	6.1	6.1	.	0	.	.	.	.	1	81.9	81.9	81.9	.	1	1.8	1.8	1.8	.

Table 4.19. Summary statistics of lower M3 dental measurements for dwarf elephant taxa from Cyprus, Crete and Tilos. Legend as Table 4.15

	Plate Count					Length (mm)					Width (mm)					Lamellar Frequency					Crown Height (mm)					Min. Crown Height (mm)					Enamel Thickness (mm)				
Species	**n**	**Mean**	**Min**	**Max**	**CV**	**n**	**Mean**	**Min**	**Max**	**CV**	**n**	**Mean**	**Min**	**Max**	**CV**	**n**	**Mean**	**Min**	**Max**	**CV**	**n**	**Mean**	**Min**	**Max**	**CV**	**n**	**Mean**	**Min**	**Max**	**CV**	**n**	**Mean**	**Min**	**Max**	**CV**
P. cypriotes	2	11.0	11	11	0.0	2	86.4	86.0	86.9	0.8	3	32.6	30.7	35.4	8.2	4	11.8	10.8	12.4	6.6	3	64.0	62.8	66.3	3.3	1	61.1	61.1	61.1	0.0	4	1.3	1.1	1.5	15.0
M. creticus	0	.	.	.	.	0	.	.	.	.	0	.	.	.	.	0	.	.	.	.	0	.	.	.	.	0	.	.	.	.	0	.	.	.	.
P. tiliensis	0	.	.	.	.	0	.	.	.	.	1	49.1	49.1	49.1	0.0	1	8.1	8.1	8.1	0.0	0	.	.	.	.	0	.	.	.	.	1	1.6	1.6	1.6	.

Table 4.20. Summary statistics of upper M3 dental measurements for dwarf elephant taxa from Cyprus, Crete and Tilos. Legend as Table 4.15

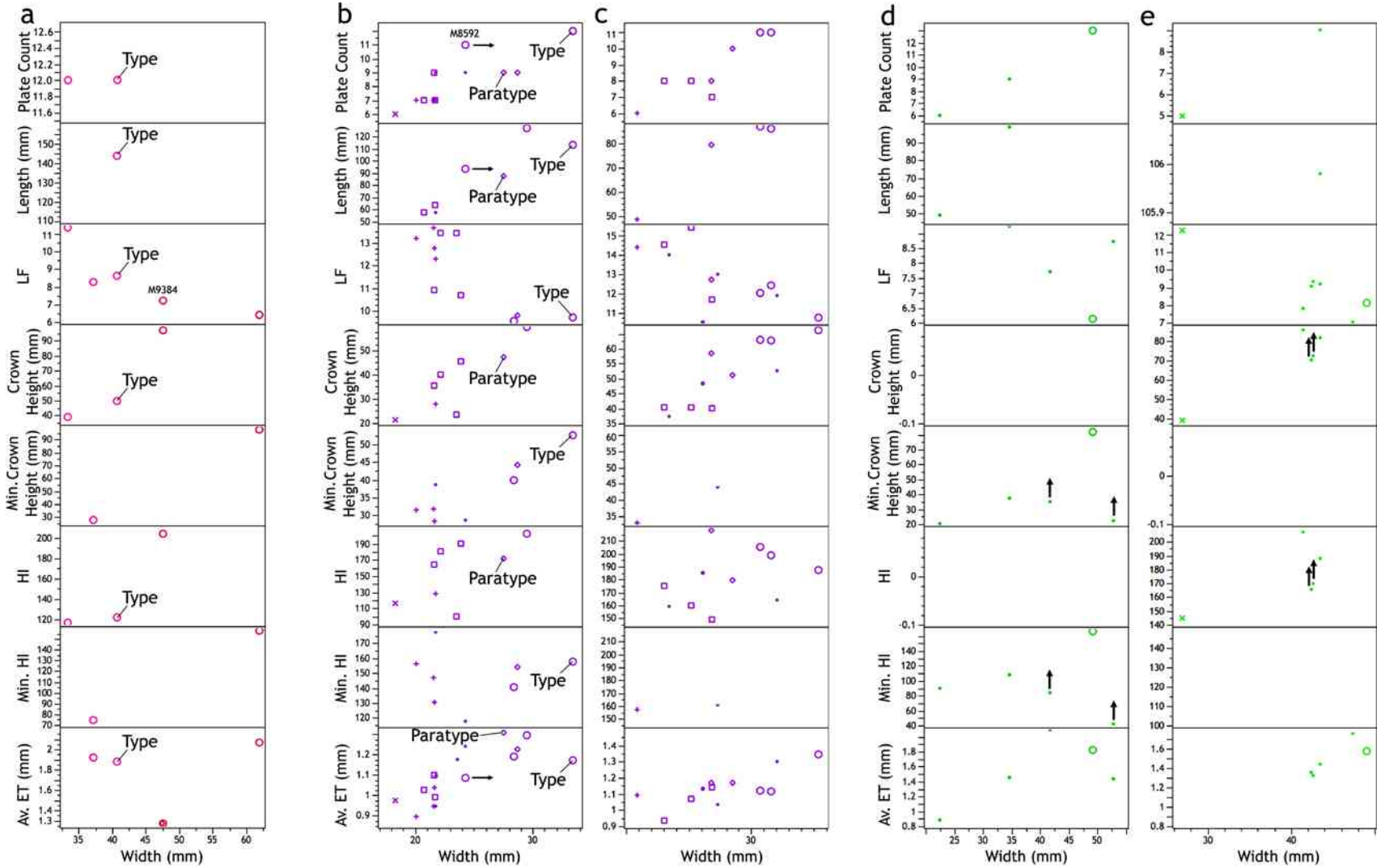

Figure 4.21. Molar variation in dwarf elephants from Crete, Cyprus and Tilos. a. Cretan lower molars (upper molars were considered too fragmentary to include in this study). **b.** Lower and **c.** Upper molars from Cyprus. **d.** Lower and **e.** Upper molars from Tilos. Arrows indicate direction, but not magnitude, of predicted value for points whose value is a likely underestimate. **Y** is dP2, **X** is dP3, **+** is dP4, opens squares are M1, open diamonds are M2, open circles are M3. Types fixed by Osborn (1942) are indicated.

an outlier for molar width (and possibly molar length), however, this specimen is encased within the mandible, and these measures are probably underestimates (M8592 was identified as M3 based on curvature and the presences of a bony 'plug' in the mandible posterior to the tooth thus its smaller size is unlikely to be due to mis-identification). The material at Imbohary is thus consistent with the presence of a single species, and the validity of *P. cypriotes* is supported.

Tilos

Very few *P. tiliensis* (Theodorou *et al.* 2007) molar specimens were available for study, and those that were are highly fragmentary. Few specimens were therefore identifiable to a position in the molar series. Bivariate scatter plots of the available material provide little taxonomic information, although they are consistent with an ontogenetic series of a single species (Figure 4.21d&e). The molar syntype, T3272, was not available for study, and the most complete M3 was a well worn lower molar (unlabelled specimen; my reference 'TmolA'). This specimen was worn into the paired root region of the tooth, and had a plate count of ∞11 or ∞10x: the plate count of 13 given for this specimen is reconstructed and may be overly conservative. The minimum crown height shown in Table 4.19 has also been excluded from comparisons with other mOTUs as it is likely to be a significant underestimate.

The majority of the *P. tiliensis* syntypes are post-cranial specimens (Theodorou *et al.* 2007). Although the full syntype series was not assessed, a large number of referred specimens from the type locality of Charkadio Cave permitted a consideration of the post-cranial variation in *P. tiliensis*. Bi- and univariate variation, and size-ratios of putative 'males' to putative 'females' are consistent with a single, sexually dimorphic taxa (Appendix 5). Thus, although variation in potentially dimorphic characters is not recommended for species delineation (Cope & Lacey 1995) post-cranial variation in *P. tiliensis* is consistent with a single species hypothesis and this taxon is considered valid.

4.3.4. Additional patterns of morphological variation in Sicilian and Maltese taxa

Qualitative molar character variation in Sicilian and Maltese taxa

Qualitative dental characters show state variation within dwarf mOTUs and *P. antiquus* (Figure 4.22, Tables 4.21 & 4.22), suggesting these characters have limited use in dwarf elephant species diagnosis. Instead, character frequencies show interesting trends that appear to be linked to the dwarfing process (see below), or to ancestry. As sample sizes are small for dwarf mOTUs, using trait frequency to differentiate between mOTUs is premature. Moreover, this would provide no independent support for phenetic groupings, as these groupings would have to be used *a priori* to define the limits of an mOTU for which trait frequency was then calculated. Instead, frequencies were converted into multi-state characters as described above, in an effort to capture the variable nature of traits whilst acknowledging the limits of sample sizes, and used to make comparisons between

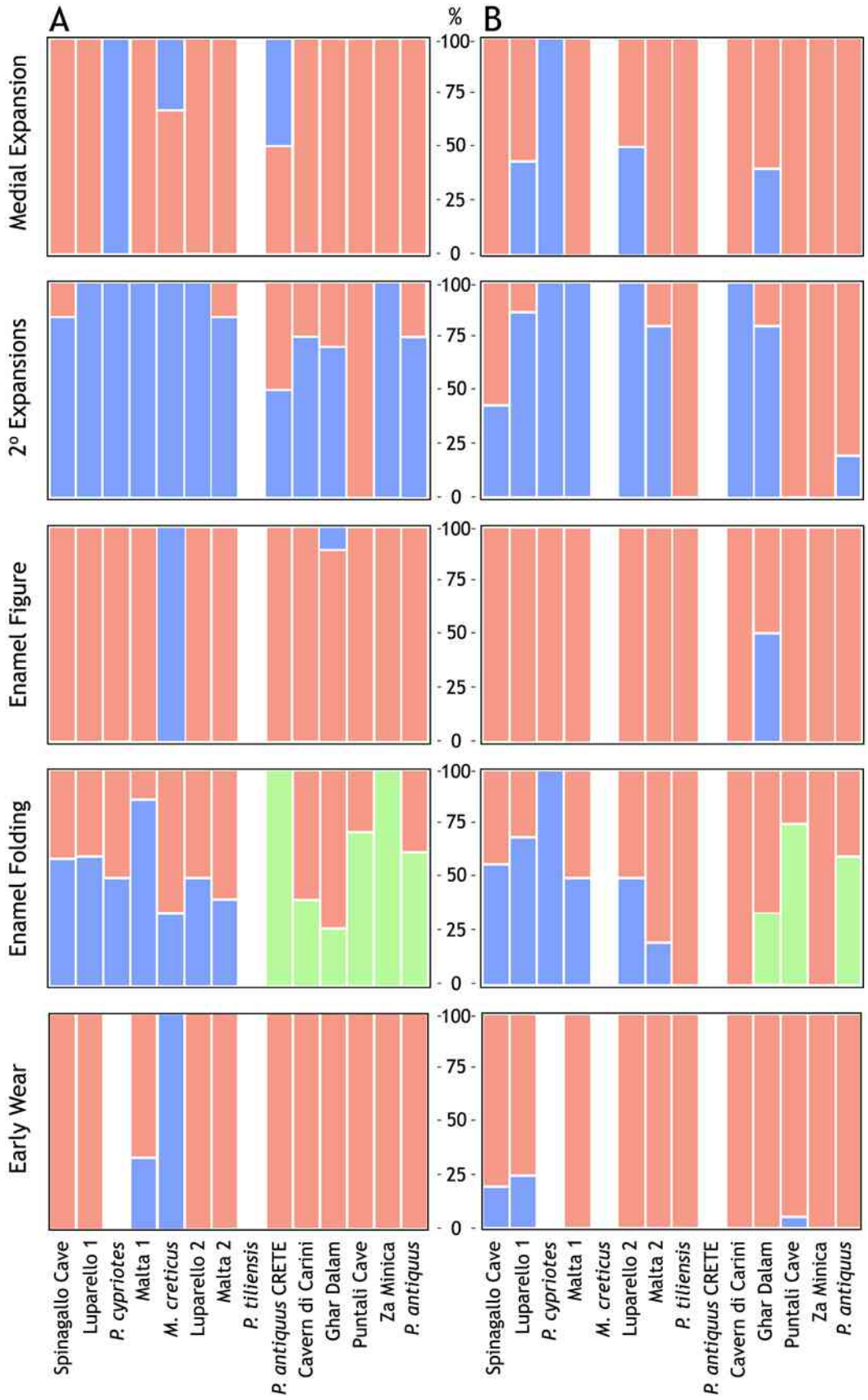

Figure 4.22. Qualitative trait frequency in [A] lower and [B] upper M3s. mOTUs are ordered, from left to right, by increasing molar width (with the exception of upper M3 Spinagallo Cave and Luparello 1, where the order is inverted). Blue is character state 0, red is 1 and green is 2. Absolute numbers are given in Tables 4.24 & 4.25.

	% Sample Showing Character State																					
	Medial Expansion				2° Expansion				Enamel Figure				Enamel Folding						Early Wear			
	0		1		0		1		0		1		0		1		2		0		1	
Malta1	0	.	100	(7)	100	(7)	0	.	0	.	100	(7)	86	(6)	14	(1)	0	.	33	(1)	67	(2)
Spinagallo Cave	0	.	100	(12)	83	(10)	17	(2)	0	.	100	(12)	58	(7)	42	(5)	0	.	0	.	100	(8)
Luperello 1	0	.	100	(4)	100	(4)	0	.	0	.	100	(4)	60	(3)	40	(2)	0	.	0	.	100	(2)
Luperello 2	0	.	100	(5)	100	(5)	0	.	0	.	100	(5)	50	(2)	50	(2)	0	.	0	.	100	(2)
Malta2	0	.	100	(6)	83	(5)	17	(1)	0	.	100	(5)	40	(2)	60	(3)	0	.	0	.	100	(4)
Ghar Dalam	0	.	100	(10)	70	(7)	30	(3)	11	(1)	89	(8)	0	.	73	(8)	27	(3)	0	.	100	(11)
Cavern di Carini	0	.	100	(5)	20	(1)	80	(4)	0	.	100	(5)	0	.	60	(3)	40	(2)	0	.	100	(5)
Puntali Cave	0	.	100	(14)	0	.	100	(14)	0	.	100	(14)	0	.	29	(4)	71	(10)	0	.	100	(14)
Za Minica	0	.	100	(1)	100	(1)	0	.	0	.	100	(1)	0	.	0	.	100	(1)	0	.	100	(1)
P. cypriotes	100	(4)	0	.	100	(4)	0	.	0	.	100	(4)	50	(2)	50	(2)	0	.	.	.	.	.
P. tiliensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. antiquus CRETE	0	.	100	(2)	50	(1)	50	(1)	0	.	100	(2)	0	.	0	.	100	(2)	0	.	100	(1)
M. creticus	33	(1)	67	(2)	100	(3)	0	.	100	(2)	0	.	33	(1)	67	(2)	0	.	100	(3)	0	.
P. antiquus	0	.	100	(14)	75	(9)	25	(3)	0	.	100	(11)	0	.	38	(5)	62	(8)	0	.	100	(11)

Table 4.21. Qualitative dental character state frequencies in lower M3s of *P. antiquus* and dwarf elephant mOTUs. Percentage and absolute numbers (in parentheses) of individuals suitable for scoring for each character state of the 5 qualitative dental characters.

	% Sample Showing Character State																					
	Medial Expansion				2° Expansion				Enamel Figure				Enamel Folding						Early Wear			
	0		1		0		1		0		1		0		1		2		0		1	
Malta1	0	.	100	(2)	100	(2)	0	.	0	.	100	(2)	50	(1)	50	(1)	0	.	0	.	100	(2)
Spinagallo Cave	0	.	100	(7)	43	(3)	57	(4)	0	.	100	(7)	57	(4)	43	(2)	0	.	20	(1)	80	(4)
Luperello 1	43	(3)	57	(4)	86	(5)	14	(1)	0	.	100	(6)	71	(5)	29	(2)	0	.	25	(1)	75	(3)
Luperello 2	50	(2)	50	(2)	100	(4)	0	.	0	.	100	(3)	50	(2)	50	(2)	0	.	0	.	100	(2)
Malta2	0	.	100	(5)	80	(4)	20	(1)	0	.	100	(4)	20	(1)	80	(4)	0	.	0	.	100	(3)
Ghar Dalam	40	(2)	60	(3)	80	(4)	20	(1)	50	(2)	50	(2)	0	.	67	(4)	33	(2)	0	.	100	(4)
Cavern di Carini	0	.	100	(2)	100	(2)	0	.	0	.	100	(2)	0	.	100	(2)	.	.	0	.	100	(1)
Puntali Cave	0	.	100	(24)	8	(2)	100	(22)	0	.	100	(24)	0	.	25	(6)	75	(18)	6	(1)	94	(17)
Za Minica	0	.	100	(1)	0	.	100	(1)	0	.	100	(1)	0	.	100	(1)	.	.	0	.	100	(1)
P. cypriotes	100	(4)	0	.	100	(4)	0	.	0	.	100	(3)	100	(4)	0	.	0	.	.	.	.	.
P. tiliensis	0	.	100	(1)	0	.	100	(1)	0	.	100	(1)	0	.	100	(1)	0	.	0	.	100	(1)
M. creticus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. antiquus	0	.	100	(5)	20	(1)	80	(1)	0	.	100	(5)	0	.	40	(2)	60	(3)	0	.	100	(5)

Table 4.22. Qualitative dental character state frequencies in upper M3s of *P. antiquus* and dwarf elephant mOTUs. Legend as Table 4.21.

	OTU Character Coding				
	Medial Expansion	2° Expansion	Enamel Figure	Enamel Folding	Early Wear
M. meridionalis	1	.	0	1	0
L. atlantica	2	.	2	2	2
P. iolensis	2	.	2	2	2
Malta1	2	0	2	1	1
Spinagallo Cave	2	1	2	1	1
Luperello 1	1	1	2	1	1
Luperello 2	1	0	2	1	2
Malta2	2	1	2	1	2
Ghar Dalam	1	1	1	1-2	2
Cavern di Carini	2	1	2	2	2
Puntali Cave	2	2	2	2	1
Za Minica	2	1	2	2	2
P. cypriotes	0	0	2	1	.
P. tiliensis	2	2	2	1	2
M. creticus	1	0	0	1	0
P. antiquus CRETE	1	1	2	2	2
P. antiquus	2	1	2	2	2

Table 4.23. Character coding for OTUs. Character frequencies from Tables 4.21 & 4.22 and species diagnoses from Maglio (1973) (grey shaded taxa) were converted to multistate characters after Table 4.4.

mOTUs (Table 4.22). However, this did not solve the problem of diagnostic ability, and qualitative dental characters were unable to arbitrate between phenetic grouping hypotheses for Malta and Sicily.

Spinagallo Cave and Malta 1 M3s all show the presence of a medial expansion, whereas Luparello 1 upper M3s sometimes do not (Table 4.23). Conversely, both Luparello 1 and Spinagallo Cave upper M3s sometimes show secondary expansions, whereas Malta 1 molars do not (Table 4.23). Spinagallo Cave also shows a higher frequency of secondary expansions than Luparello 1 (Figure 4.22). A combined Malta 1-Sicily 1 sample would be coded as '1' for each of these characters; such character variation is seen in a number of mOTUs and is acceptable within-taxon variation. Differences between mOTUs in these characters provide conflicting evidence for their taxonomic grouping, but sample sizes are low (particularly Malta 1 upper M3s, Table 4.22), and if the absence of medial expansions and presence of secondary expansion is occurring at a low frequency in the population, these character states may not have been sampled.

As with the 'small-sized' Sicilian and Maltese dwarf elephants, Luparello 2 and Malta 2 differ in the frequency of the presence of medial and secondary expansions (Table 4.21, Figure 4.22). Secondary expansions are always absent, and medial expansions sometimes absent in Luparello 2, where in Malta 2 they are sometimes and always present, respectively (Figure 4.22). The lower frequency or absence of expansions in Luparello 2 may relate to the more simplified enamel in this sample relative to Malta 2 (Malta 2 has a higher proportion of folded enamel, Figure 4.22, although absolute numbers are low, Tables 4.21 & 4.22). These differences may support taxonomic discrimination but, given size-related trends (see below), low sample number, and the potential for within-taxon variability, this support is fairly limited.

Within Sicily 3, the only differences between its constituent mOTUs character codes are in Puntali Cave secondary expansions and early wear pattern (Table 4.23). Za Minica and C. di Carini show a mixed character state for secondary expansions, whereas in Puntali Cave material these are always present. Za Minica has a sample size of one for both upper and lower M3s (Tables 4.21 & 4.22), and thus the frequency of character states cannot be ascertained. C. di Carini has a high frequency of teeth lacking the secondary expansions (Figure 4.22), which may point to some differences between this mOTU and Puntali Cave. The coding for a combined Sicily 3 sample would be identical to that of *P. antiquus*, except for a single Puntali Cave molar showing a sub-equal early wear pattern (Table 4.22). However, this indivdual may not be in a sufficiently early stage of wear (in later wear *P. antiquus* often show more equal, or only slightly sub-equal worn loops). This may also account for the variability in this character observed in Malta 1, Spinagallo Cave and Luparello 1. Sicily 3 constituent mOTUs all show more highly folded enamel than Luparello 2 or Malta 2 (Figure 4.22; note the transition from blue/red bars to red/green bars), supporting the separation of these taxa. Again, however, as a number of individual specimens in each mOTU are scored as character state '1' (Tables 4.21 & 4.22), diagnostic use of this character is limited.

Phenetic grouping has suggested that multiple taxa are present in the Ghar Dalam material, and

the variability of qualitative characters could add weight to this (Figure 4.22). These differences also support delineation from Sicily 3. However, variability in the presence/absence of medial and secondary expansions seems common in dwarf elephant taxa, and may relate to dwarfing trends. Apart from *M. creticus*, Ghar Dalam is the only mOTU to include specimens which do not show the typical *Palaeoloxodon* lozenge-shaped enamel figure. The three specimens scored as 0 for this trait all show enamel figures that have a 'stepped' figure, with distorted mid-sections. All specimens show 'medial' expansions, offset from the medial position due to this distortion, suggesting it may be owing to fabricational noise (*sensu* Roth 1989). Two specimens (GD 1018 and GD 1057) also show the typical *Palaeoloxodon* early wear pattern; the third specimen (GD 1058) cannot be scored for this character. Thus, for these specimens, I suggest the absence of a lozenge-shaped enamel figure carries little taxonomic weight.

Relative size-change in Sicilian and Maltese dental and post-cranial material

Post-cranial variation is consistent with (i) the presence of three different-sized taxa on Sicily and Malta, (ii) with only one taxon within the type and referred material of *P. falconeri* and *'P. melitensis'* and (iii) with the presence of two taxa at Luparello Cave, in line with molar evidence (Appendix 5). Alone, the relative size of Sicilian and Maltese M3s (Table 4.24) and long-bones (Tables 4.25-4.28) compared with *P. antiquus* provides little additional information on the conspecifity of mOTUs (all are compared with the same full-size 'standard', and % values simply reiterate absolute similarities between mOTUs). Comparing the amount of size-change in M3s relative to post-crania across mOTUs (Table 4.29) does, however, inform the taxonomic debate.

Spinagallo Cave and Luparello 1 show similar levels of relative size reduction in upper and lower M3 comparisons with 'male' and 'female' post-crania, if the 'small-sized' dimorphic taxon hypothesis is employed for Luparello 1 (top two rows of each mOTU, Table 4.29; sexes were identified following Appendix 5). A similar degree of relative size reduction suggests a similar pattern of evolution of small body size, which when combined with the absolute levels of similarity supports conspecifity between these taxa. However, size-reduction in teeth and post-crania has also been linked with time of isolation (Lister 1996a) and a similar degree of relative and absolute size-reduction between taxa could relate to this and have evolved in parallel. If taxa are contemporaneous (as Luparello 1 and Spinagallo Cave may be, based on the available evidence; see Chapter 2), and isolation/insularity linked with glacial-interglacial cycles, then isolation time is expected to be the same. Nevertheless, relative size-reduction does not provide evidence for taxonomic discrimination between these taxa (although if further evidence showed Luparello 1 dental material to be associated with the 'large-sized' post-crania, conspecifity with Spinagallo 1 would not be supported).

If post-crania grouped as the 'small-sized' dimorphic Maltese taxon is equated with Malta 1, conspecificity with Spinagallo Cave and Luparello 1 is not supported: post-cranial sizes are similar, but as Malta 1 M3s are slightly larger than Luparello 1 and Spinagallo Cave M3s, the relative size-

		Spinagallo Cave	Luparello 1	Malta 1	Luperello 2	Malta 2	Ghar Dalam	Cavern di Carini	Puntali Cave	Za Minica	*P. cypriotes* 1	*P. cypriotes* 2	*P. antiquus* CRETE	*P. tiliensis*	*M. creticus*
Lower M3															
Width	n	12	4	8	6	7	10	2	5	1	4	4	2	1	3
	% mean	34.1	34.9	39.9	53.8	59.7	73.9	73.7	80.8	89.0	37.5	27.6	71.2	63.9	38.5
	% min	21.4	25.2	29.4	40.3	46.8	51.5	57.5	67.4	75.7	26.8	21.3	52.6	54.4	29.0
	% max	49.0	53.6	59.0	79.2	66.0	107.7	102.5	105.0	114.2	55.7	34.8	103.3	82.0	53.2
Length	n	3	2	1	4	1	2	1	0	0	3	3	0	0	1
	% mean	27.3	24.2	37.1	39.6	49.5	50.1	70.4	.	.	29.5	.	.	.	51.0
	% min	23.4	21.7	35.8	34.8	47.8	39.7	68.1	.	.	23.9	.	.	.	43.0
	% max	34.0	28.6	41.1	47.2	54.8	65.6	78.0	.	.	37.3	.	.	.	57.6
Crown Height	n	4	4	3	3	3	2	0	1	0	1	1	1	0	2
	% mean	29.2	33.2	29.4	45.7	51.4	68.7	.	71.5	.	37.1	32.1	60.3	.	36.8
	% min	22.3	23.8	34.1	32.8	39.0	61.7	.	65.7	.	34.1	29.0	55.4	.	26.5
	% max	34.4	40.7	33.5	55.6	64.5	76.3	.	77.7	.	40.3	34.1	65.5	.	53.9
Min. Crown Height	n	6	0	4	3	4	7	3	6	1	2	2	1	1	1
	% mean	32.9	.	35.3	46.7	42.9	66.2	65.4	70.6	77.0	30.6	.	64.7	54.2	.
	% min	24.6	.	24.9	37.2	28.0	45.8	43.8	55.5	62.9	21.6	.	52.8	44.3	.
	% max	46.0	.	49.1	53.3	56.1	83.2	85.2	83.0	86.2	39.0	.	72.4	60.7	.
Upper M3															
Width	n	8	7	3	3	9	3	3	19	2	3	3	0	1	0
	% mean	37.7	32.9	43.1	54.4	61.1	81.5	74.1	82.0	82.7	40.7	30.9	.	61.3	.
	% min	28.9	24.8	35.4	43.5	45.9	63.0	61.4	63.6	70.1	33.4	27.2	.	53.3	.
	% max	51.8	39.7	52.2	68.9	77.2	110.1	92.0	113.8	98.6	51.3	35.8	.	71.1	.
Length	n	0	5	0	3	5	1	1	6	0	2	2	0	0	0
	% mean	.	34.3	.	53.3	60.5	60.3	75.8	74.6	.	29.6	30.9	.	.	.
	% min	.	26.0	.	44.3	52.5	52.9	66.5	59.2	.	25.9	28.3	.	.	.
	% max	.	46.6	.	67.3	72.6	71.8	90.2	105.2	.	35.4	35.5	.	.	.
Crown Height	n	5	5	1	4	2	4	1	7	2	3	3	0	0	0
	% mean	40.1	36.7	43.8	56.9	59.7	84.6	82.7	84.6	89.0	38.0	31.9	.	.	.
	% min	29.5	28.0	38.0	42.8	51.1	64.3	71.9	67.5	76.3	32.4	28.4	.	.	.
	% max	51.8	51.1	52.7	84.1	73.0	114.3	99.6	116.4	108.6	47.3	37.9	.	.	.
Min. Crown Height	n	3	2	2	0	5	2	0	6	0	1	1	0	0	0
	% mean	37.8	38.9	35.3	.	64.8	71.4	.	77.9	.	35.9	.	.	.	.
	% min	23.8	27.5	23.9	.	43.3	48.7	.	55.0	.	26.4	.	.	.	.
	% max	51.5	46.8	44.0	.	80.4	88.7	.	94.6	.	41.6	.	.	.	.
Grand Mean % (L)		30.9	27.5	35.4	46.4	50.9	64.75	69.87	74.29	83.0	33.7	29.9	65.38	59.0	42.1
Grand Mean % (U)		38.5	35.7	40.7	54.9	61.5	74.47	77.5	79.78	85.86	36.1	31.2	.	61.3	.

Table 4.24 Dwarf elephant M3 measures as a percentage of their putative full-sized ancestor. Mean, minimum and maximum values for dwarf elephant mOTUs are presented as a percentage of full-sized *M. meridionalis* (*M. creticus*), *P. iolensis* (*P. cypriotes* 2), or *P. antiquus* (all other dwarf taxa; whilst *P. antiquus* cannot be confirmed as the putative ancestor for these dwarf taxa, *Palaeoloxodon* affinity is likely. *P. antiquus* is taken as the full-sized reference standard for this genus). % mean, is the mean dwarf value as a percentage of the mean full-size value; % min is the 'minimum percentage', and is the minimum dwarf value as a percentage of the maximum full-size value; % max is the 'maximum percentage', and is the maximum dwarf value as a percentage of the minimum full-size value. Blue shading indicates the highest % max (= min. possible size-change), and orange shading the lowest % min (= max. possible size change) for each mOTU, highlighting this potential range. Grand Means of % changes for all measures are used for comparisons with post-crania.

Humerus		*P. antiquus*	Spinagallo Cave		Luparello Cave			Malta			Puntali Cave		S3	*P. tiliensis*	
		.	F	M	Small F	Small M/ Large F	Large M	Small F	Small M/ Large F	Large M	F	M	.	F	M
DL	n	10	2	5	.	.	1	1	.	.	.	6	4	3	3
	Mean	862	176	240	.	.	347	203	.	.	.	468	491	343	401
	Min	700	173	212	.	.	347	203	.	.	.	439	468	323	392
	Max	1061	179	260	.	.	347	203	.	.	.	530	525	369	416
	% mean	.	20.4	27.8	.	.	40.2	23.5	.	.	.	54.3	56.9	39.7	46.5
	% min	.	16.3	20.0	.	.	32.7	19.1	.	.	.	41.4	44.1	30.4	36.9
	% max	.	25.6	37.1	.	.	49.6	29.0	.	.	.	75.7	75.0	52.7	59.4
PML	n	6	3	4	.	.	.	1	1	.	.	5	4	4	2
	Mean	267.7	65.4	85.2	.	.	.	51.4	82.0	.	.	164.0	155.5	109.8	132.5
	Min	230.0	62.6	79.6	.	.	.	51.4	82.0	.	.	151.0	145.0	104.0	123.0
	Max	321.0	66.9	87.9	.	.	.	51.4	82.0	.	.	177.0	169.0	117.1	142.0
	% mean	.	24.4	31.8	.	.	.	19.2	30.6	.	.	61.3	58.1	41.0	49.5
	% min	.	19.5	24.8	.	.	.	16.0	25.5	.	.	47.0	45.2	32.4	38.3
	% max	.	29.1	38.2	.	.	.	22.3	35.7	.	.	77.0	73.5	50.9	61.7
Head AP	n	9	4	6	.	.	1	.	2	2	.	6	4	3	2
	Mean	246.9	61.2	77.8	.	.	118.0	.	80.0	124.0	.	137.3	134.0	97.3	112.6
	Min	188.0	57.8	71.8	.	.	118.0	.	70.7	116.0	.	130.0	129.0	94.7	109.2
	Max	285.0	64.2	83.6	.	.	118.0	.	89.4	132.0	.	148.0	138.0	102.1	116.0
	% mean	.	24.8	31.5	.	.	47.8	.	32.4	50.2	.	55.6	54.3	39.4	45.6
	% min	.	20.3	25.2	.	.	41.4	.	24.8	40.7	.	45.6	45.3	33.2	38.3
	% max	.	34.2	44.5	.	.	62.8	.	47.5	70.2	.	78.7	73.4	54.3	61.7
DML	n	9	13	12	1	.	1	.	.	.	.	5	4	6	3
	Mean	310.3	76.7	98.7	75.2	.	137.0	.	.	.	.	185.8	185.0	120.7	150.5
	Min	257.0	68.8	87.8	75.2	.	137.0	.	.	.	.	177.0	176.0	117.1	144.6
	Max	373.0	83.5	111.3	75.2	.	137.0	.	.	.	.	205.0	192.0	123.6	159.0
	% mean	.	24.7	31.8	24.2	.	44.1	.	.	.	.	59.9	59.6	38.9	48.5
	% min	.	18.4	23.5	20.2	.	36.7	.	.	.	.	47.5	47.2	31.4	38.8
	% max	.	32.5	43.3	29.2	.	53.3	.	.	.	.	79.8	74.7	48.1	61.9
Grand Mean %			23.6	30.7	24.2	.	44.1	21.4	31.5	50.2	.	57.8	57.2	39.8	47.5

Table 4.25. Dwarf elephant humerus measures as a percentage of their putative full-size ancestor. % calculations, shading and 'ancestor' choice as described in Table 2.24. Measurement abbreviations as Table 4.3. Measurements were selected to maximize mOTU inclusion. Samples are divided into putative sex groups following Appendix 5; F is female, M is Male. No sex information is available for full-size comparator *P. antiquus*. Luparello Cave and Maltese material is divided into three size classes, consistent with two different, overlapping dimorphism hypotheses (Appendix 5) and gender attribution only pertains within each dimorphism hypothesis. Puntali Cave material is divided into two sexes, but it should be noted that this dimorphism hypothesis received limited support (Appendix 5). S3 includes material attributed to 'Sicily 3' based on phenetic clustering, for which locality information is limited to 'Sicily'.

		P. antiquus	Spinagallo Cave		Luparello Cave			Puntali Cave		ZM	S3	*P. tiliensis*	
Ulna		.	F	M	Small F	Small M/ Large F	Large M	F	M	.	.	F	M
DL	n	6	14	2	.	.	.	.	4	1	4	5	3
	Mean	684	153	191	.	.	.	.	324	381	348	268	323
	Min	530	140	184	.	.	.	.	314	381	330	249	309
	Max	801	162	198	.	.	.	.	330	381	378	291	333
	% mean	.	22.4	27.9	.	.	.	.	47.4	55.7	50.8	39.1	47.2
	% min	.	17.5	23.0	.	.	.	.	39.2	47.6	41.2	31.1	38.6
	% max	.	30.6	37.4	.	.	.	.	62.3	71.9	71.3	54.9	62.8
MDML	n	6	18	2	.	1	1	.	4	1	3	5	4
	Mean	134.1	27.8	36.6	.	36.1	55.0	.	76.2	81.0	78.0	44.7	51.9
	Min	108.0	25.6	36.2	.	36.1	55.0	.	74.0	81.0	75.0	39.3	50.8
	Max	164.0	32.3	37.0	.	36.1	55.0	.	80.0	81.0	80.0	50.9	53.2
	% mean	.	20.7	27.3	.	26.9	41.0	.	56.8	60.4	58.2	33.4	38.7
	% min	.	15.6	22.1	.	22.0	33.5	.	45.1	49.4	45.7	24.0	31.0
	% max	.	29.9	34.3	.	33.4	50.9	.	74.1	75.0	74.1	47.2	49.3
DAP	n	5	14	2	1	.	.	.	3	1	4	4	4
	Mean	210.6	48.4	63.6	48.2	.	.	.	97.7	123.0	117.0	80.0	100.3
	Min	168.0	42.3	62.0	48.2	.	.	.	93.0	123.0	110.0	69.9	95.4
	Max	266.0	53.4	65.2	48.2	.	.	.	102.0	123.0	120.0	87.3	103.8
	% mean	.	23.0	30.2	22.9	.	.	.	46.4	58.4	55.6	38.0	47.6
	% min	.	15.9	23.3	18.1	.	.	.	35.0	46.2	41.4	26.3	35.9
	% max	.	31.8	38.8	28.7	.	.	.	60.7	73.2	71.4	52.0	61.8
	Grand Mean %		22.0	28.5	22.9	26.9	41.0	.	50.2	58.2	54.8	36.8	44.5

Table 4.26. Dwarf elephant ulna measures as a percentage of their putative full-size ancestor. Legend as Table 4.25; ZM is Za Minica.

reduction ratios are much higher in Malta 1 (Table 4.29). This is indicative of a different evolutionary history between Malta 1 and the other small-sized taxa, and may indicate phyletic independence of these taxa, or a difference in isolation time, or both.

Relative size reduction also supports the discrimination of Malta 2 and Luparello 2 from Sicily 3. Sicily 3's constituent mOTUs are consistent with each other in relative size reduction (and, where molar material is not available, post-cranial grand mean % values are comparable, Tables 4.25-4.28), but at odds with size reduction ratios for Malta 2 and Luparello 2, regardless of the post-cranial/dental combinations chosen for these latter taxa (Table 4.29). The size-reduction ratios are most different when 'male' Puntali Cave values are compared with 'large male' values for Luparello 2 and Malta 2 (i.e. when the most similar-sized post-crania are compared, Table 4.29). If dental material is hypothesized to be associated with the large post-cranial taxa (dimorphic or unknown sex), Luparello 2 and Malta 2 show similar relative size-reduction ratios to each other, supporting their phenetic grouping.

4.3.5. Size-change and size-related trends

Patterns of size-reduction

Mosaic evolution of dwarf elephant morphology is apparent in the relative size-reduction of upper M3s, lower M3s and post-crania (Table 4.29). In all mOTUs, upper M3s have become dwarfed to a lesser degree than lower M3s (upper M3s grand means are a higher % of the full-size 'ancestor' mean; Table 4.29), although this difference is less clear for *P. tiliensis*. This trend is seen in all individual molar size variables, as well as the grand means, and crown height percentages show the greatest discrepancy between lower and upper M3s (Table 4.24; as reliable crown heights are lacking for *P. tiliensis*, this might explain why upper and lower M3 % Grand Mean are more similar for this taxa).

In general, post-cranial material shows a greater degree of size reduction than molar material (Table 4.29), a common phenomenon in insular dwarfs (Gould 1975, Lister 1996). The only examples of a relative size-reduction ratio of less than 1 (indicating teeth are more reduced in size than post-crania) are in the combinations of 'large male' post-crania with Malta 1 and Malta 2, and this material may not be associated. Sexual dimorphism in post-crania (Appendix 5), but not in teeth, results in different relative size-reduction ratios for putative sexes, and inter-sex differences are increased where dimorphism ratios are higher (e.g. in Spinagallo Cave vs *P. tiliensis*, Table A5.2). This is due to comparisons with a mixed sex full-sized comparator sample (based on sex-identification in Kroll (1991)); mean values of dwarf post-crania as a percentage of the full-sized ancestor are likely to be underestimated for females and overestimated for males. Had it been possible, comparisons should have been made between individuals of the same sex, where size-reduction ratios would be expected to be similar (assuming the degree of dimorphism remains the same). When there is limited evidence

		P. antiquus	Spinagallo Cave		Malta			Puntali Cave		S3	*P. tiliensis*		*P. cypriotes*
Femur		.	F	M	Small F	Small M/ Large F	Large M	F	M	.	F	M	.
DL	n	4	7	4	.	.	1	0	9	3	3	2	.
	Mean	1059	267	327	.	.	445		596	558	448	527	.
	Min	1005	250	307	.	.	445		560	535	438	516	.
	Max	1153	280	349	.	.	445		650	605	462	538	.
	% mean	.	30.9	30.9	.	.	42.0		56.3	52.7	42.3	49.7	.
	%min	.	21.7	26.6	.	.	38.6		48.6	46.4	38.0	44.8	.
	% max	.	27.9	34.7	.	.	44.3		64.7	60.2	46.0	53.5	.
MDAP	n	5	15	8	.	.	2	1	9	3	4	2	.
	Mean	152.3	35.5	43.1	.	.	76.5	63.0	87.8	87.3	54.2	64.3	.
	Min	136.0	32.0	39.6	.	.	72.0	63.0	81.0	85.0	51.8	62.4	.
	Max	167.0	41.3	49.9	.	.	81.0	63.0	99.0	92.0	58.5	66.1	.
	% mean	.	23.3	28.3	.	.	50.2	41.4	57.7	57.4	35.6	42.2	.
	%min	.	19.2	23.7	.	.	43.1	37.7	48.5	50.9	31	37.4	.
	% max	.	30.3	36.7	.	.	59.6	46.3	72.8	67.6	43	48.6	.
DML	n	3	18	10	.	.	2	1	10	3	3	2	1
	Mean	302.3	65.2	81.1	.	.	127.5	114.0	149.4	149.0	110.1	132.9	90.0
	Min	283.0	56.6	74.0	.	.	125.0	114.0	127.0	147.0	106.8	129.0	90.0
	Max	320.0	71.5	86.3	.	.	130.0	114.0	164.0	153.0	113.0	136.9	90.0
	% mean	.	21.6	26.8	.	.	42.2	37.7	49.4	49.3	36.4	44.0	29.8
	%min	.	17.7	23.1	.	.	39.1	35.6	39.7	45.9	33.4	40.3	28.1
	% max	.	25.3	30.5	.	.	45.9	40.3	58.0	54.1	39.9	48.4	31.8
	Grand Mean %		25.3	28.7	.	.	44.8	39.5	54.5	53.1	38.1	45.3	29.8

Table 4.27. Dwarf elephant femur measures as a percentage of their putative full-size ancestor. Legend as Table 4.25.

		P. antiquus	Spinagallo Cave		Luparello Cave			Malta			Puntali Cave		ST	S3	*P. tiliensis*	
Tibia		.	F	M	Small F	Small M/ Large F	Large M	Small F	Small M/ Large F	Large M	F	M	.	.	F	M
DL	n	8	37	11	1	.	1	.	.	1	1	16	2	2	16	7
	Mean	633	149	196	156	.	234	.	.	315	270	339	366	364	267	317
	Min	502	135	181	156	.	234	.	.	315	270	315	362	356	250	298
	Max	700	162	214	156	.	234	.	.	315	270	378	369	371	290	339
	% mean	.	23.6	30.9	24.6	.	37.0	.	.	49.8	42.7	53.6	57.7	57.4	42.2	50.1
	% min	.	19.3	25.9	22.3	.	33.4	.	.	45.0	38.6	45.0	51.7	50.9	35.7	42.6
	% max	.	32.3	42.6	31.1	.	46.6	.	.	62.7	53.8	75.3	73.5	73.9	57.8	67.5
MDAP	n	7	37	11	1	.	1	.	.	2	1	14	2	2	17	8
	Mean	110.1	28.3	37.1	26.9	.	42.0	.	.	49.5	50.0	61.4	71.5	61.5	45.5	57.6
	Min	81.0	23.6	32.5	26.9	.	42.0	.	.	47.0	50.0	54.0	68.0	61.0	40.1	52.3
	Max	122.0	32.4	40.6	26.9	.	42.0	.	.	52.0	50.0	69.0	75.0	62.0	54.5	64.0
	% mean	.	25.7	33.7	24.4	.	38.1	.	.	44.9	45.4	55.8	64.9	55.8	41.3	52.3
	% min	.	19.3	26.6	22.0	.	34.4	.	.	38.5	41.0	44.3	55.7	50.0	32.9	42.8
	% max	.	40.0	50.1	33.1	.	51.9	.	.	64.2	61.7	85.2	92.6	76.5	67.3	79.0
	Grand Mean %		24.6	32.3	24.5	.	37.5	.	.	47.4	44.0	54.7	61.3	56.6	41.8	51.2

Table 4.28. Dwarf elephant tibia measures as a percentage of their putative full-size ancestor. Legend as Table 4.25; ST is San Teodoro Cave

	% Full-Size		% Full-Size Post-crania						% Ratio	
mOTU	LM3	UM3	Sex	Humerus	Ulna	Femur	Tibia	GM2	LM3	UM3
Spinagallo Cave	30.9	38.5	F	23.6	22	25.3	24.6	23.9	1.29	1.61
			M	30.7	28.5	28.7	32.3	30.1	1.03	1.28
Luparello 1	27.5	35.7	Small F	24.2	22.9	.	24.5	23.9	1.15	1.5
			Small M/Large F		26.9	.	.	26.9	1.02	1.33
			Large M	44.1	41	.	37.5	40.9	0.67	0.87
Malta 1	35.4	40.7	Small F	21.4	.	.	.	21.4	1.65	1.9
			Small M/Large F	31.5	.	.	.	31.5	1.12	1.29
			Large M	50.2	.	44.8	47.4	47.5	0.75	0.86
Luparello 2	46.4	54.9	Small F	24.2	22.9	.	24.5	23.9	1.94	2.3
			Small M/Large F		26.9	.	.	26.9	1.72	2.04
			Large M	44.1	41	.	37.5	40.9	1.14	1.34
Malta 2	50.9	61.5	Small F	21.4	.	.	.	21.4	2.38	2.87
			Small M/Large F	31.5	.	.	.	31.5	1.62	1.95
			Large M	50.2	.	44.8	47.4	47.5	1.07	1.3
Ghar Dalam	64.8	74.5	.	.	.	.	.	.	.	.
C. di Carini	69.9	77.5	.	.	.	.	.	.	.	.
Puntali Cave	74.3	79.8	F	.	.	39.5	44	41.8	1.78	1.91
			M	57.8	50.2	54.5	54.7	54.3	1.37	1.47
Za Minica	83	85.6	.	.	58.2	.	.	58.2	1.43	1.47
San Teodoro Cave	.	.	.	.	.	.	61.3	61.3	.	.
Sicily 3 (other)	.	.	.	57.2	54.8	53.1	56.6	55.4	.	.
P. cypriotes 1	33.7	36.1	.	.	.	29.8	.	29.8	1.13	1.21
P. cypriotes 2	29.9	31.2	.	.	.	29.8	.	29.8	1	1.05
P. tiliensis	59.0	61.3	F	39.8	36.8	38.1	41.8	39.1	1.51	1.57
			M	47.5	44.5	45.3	51.2	47.1	1.25	1.3
P. antiquus CRETE	65.4	.	.	.	.	.	.	.	.	.
M. creticus	42.1	.	.	.	.	.	.	.	.	.

Table 4.29. Relative size reduction of teeth and post-crania in Mediterranean dwarf elephants. The grand means % of full-size ancestor are shown for lower (LM3) and upper (UM3) M3s and each long-bone. The mean of grand means (GM2) was calculated to summarize relative post-cranial size (grand means of each bone are broadly similar within a sex/mOTU). LM3 and UM3 grand mean % were divided by GM2 for each sex/mOTU to provide a measure of relative size change in teeth and post-crania. A ratio of 1 indicates teeth and post-crania have reduced in size to equal degrees (each is the same % of the full-size comparator value). A ratio greater than 1 indicates that teeth have reduced in size to a lesser extent than post-crania, and the higher the ratio the greater the relative size reduction in post-crania. A ratio less than 1 indicates that teeth have reduced in size to a greater degree than post-crania. Because Malta and Luparello Cave post-crania could not be definitively assigned to a dental mOTU, ratios are calculated for all possible mOTU/post-cranial sample combinations (based on the three size classes identified in Appendix 5). '*P. cypriotes* 2' M3 grand means are percentages of *P. iolensis*, whilst post-crania comparisons are based on *P. antiquus*. Post-cranial size of *P. iolensis* is unknown, thus the % ratio for *P. cypriotes* 2 must be treated with caution.

for the presence of two sexes (Puntali Cave, *P. cypriotes*), and/or the data fit a number of dimorphic taxon hypotheses (Luparello Cave and Malta; Appendix 5 for discussion), interpreting the size-reduction signal in relation to evolutionary hypotheses is hampered further.

These problems preclude detailed analysis of size-reduction trends, but a broad trend can be established despite this: in general, large dwarf mOTUs (Puntali Cave and Za Minica) have higher relative size-reduction ratios than smaller taxa. Using lower M3 molar width (Figure 4.23) and the distal femur (Figure 4.29) as indicators of body size, dwarf MOTUs can be ranked by size as follows (from large to small):

1. Puntali Cave (1.37) and Za Minica (1.43)
2. *P. tiliensis* (1.25)
3. Malta 2 (1.07) & Luparello 2 (1.14)
4. Malta 1 (1.12) & *P. cypriotes* (1.13/1.0[3])
5. Spinagallo Cave (1.03) and Luparello 1 (1.02)

Limiting comparisons to relative ratios based on lower M3s (as *P. tiliensis* lacks UM3 crown height, and *P. cypriotes* UM3s show shape trends that might indicate an ancestor other than *P. antiquus*), and putative males, the ranking of size-reduction ratios mirrors that of body size (size-reduction ratio given in parentheses after each mOTU), indicating covariation of absolute and relative size reductions. This may reflect a covariation of each with a third factor, such as time of isolation (as suggested for different size-reduction patterns in teeth and post-crania in Jersey and Cretan deer, and in *M. exilis* and Wrangel Island mammoths; Lister 1996a). Without further contextual evidence, however, this cannot be established.

Molar size indices

Dwarf elephant mOTUs and full-sized elephant taxa were grouped into eight overlapping size classes based on pair-wise comparisons of upper and lower M3 mean width (Figures 4.23 & 4.24). Overlap between groups emphasized the continuous variation of metric traits within and between taxa. Although the boundaries between size-classes were not identical in upper and lower teeth, differences were relatively minor and potentially related to lower sample sizes in upper M3s (Table 4.31). Eastern Mediterranean elephants were grouped with Sicilian and Maltese taxa of similar M3 width (a proxy for size), producing three broader size-classes for further trait analysis: (i) *P. cypriotes*, Luparello 1, Malta 1 and Spinagallo Cave, (ii) *P. tiliensis,* Luparello 2 and Malta 2 and (iii) *P. antiquus* CRETE, C. di Carini, Ghar Dalam, Puntali Cave and Za Minica (Figure 4.25). *M. creticus* is grouped with both (i) and (ii). *P. antiquus* CRETE also appears to overlap with group (ii), but this is

[3] A relative size-reduction ratio of 1.0 is based on M3 comparisons with *P. iolensis (to which* P. cypriotes may show greater affinity; see 4.2.5), but *P. antiquus* postcranial values, this ratio may thus be erroneous.

	Width (mm)				Hypsodonty Index				Min. HI				Length Index				Lamellar Frequency				Enamel Index			
	n	Mean	Min	Max	n	Mean	Min	Max	n	Mean	Min	Max	n	Mean	Min	Max	n	Mean	Min	Max	n	Mean	Min	Max
Spinagallo Cave	12	26.2	19.3	29.4	4	189.6	160.4	215.3	6	188.3	168.0	211.2	3	398.6	353.3	428.6	8	9.3	6.2	11.9	12	5.8	4.0	6.8
Luperello 1	4	26.8	22.8	32.2	4	200.2	177.6	230.4	0	.	.	.	1	361.7	361.7	361.7	4	9.7	6.3	11.6	4	4.2	3.9	4.5
P. cypriotes	4	28.9	24.3	33.4	1	202.6	202.6	202.6	2	149.1	140.5	157.7	3	385.5	339.7	431.6	2	9.6	9.6	9.7	4	4.1	3.5	4.5
Malta1	8	30.7	26.6	35.4	3	149.7	139.1	163.2	4	173.7	130.3	199.9	0	.	.	.	5	8.9	8.0	10.0	8	4.9	4.2	6.3
M. creticus	3	37.1	33.4	40.7	2	119.1	116.5	121.7	1	74.6	74.6	74.6	1	356.0	356.0	356.0	3	9.4	8.3	11.4	2	4.9	4.6	5.2
Luperello 2	6	41.4	36.5	47.5	3	175.8	157.3	196.9	3	171.5	161.2	184.6	4	364.1	324.0	412.8	4	9.2	7.5	11.4	4	3.6	3.3	4.0
Malta2	7	46.1	42.4	53.5	3	186.5	155.0	205.3	4	135.9	120.4	148.9	1	349.6	349.6	349.6	4	6.4	5.4	7.3	6	3.8	2.8	4.3
P. tiliensis	1	49.2	49.2	49.2	0	.	.	.	1	166.5	166.5	166.5	0	.	.	.	1	6.1	6.1	6.1	1	3.7	3.7	3.7
P. antiquus CRETE	2	54.8	47.6	62.0	1	203.8	203.8	203.8	1	157.6	157.6	157.6	0	.	.	.	2	6.8	6.4	7.2	2	3.0	2.7	3.3
Cavern di Carini	2	56.8	52.0	61.5	0	.	.	.	3	182.8	155.8	205.6	1	432.5	432.5	432.5	2	6.0	5.1	6.9	2	3.2	3.2	3.2
Ghar Dalam	10	56.9	46.6	64.6	1	198.0	198.0	198.0	7	172.2	149.5	187.1	2	355.4	332.6	378.2	14	6.3	4.6	8.2	10	3.1	2.7	3.7
Puntali Cave	5	62.2	61.0	63.0	1	201.8	201.8	201.8	3	173.9	168.5	183.6	0	.	.	.	15	5.3	4.8	6.2	5	3.2	2.9	3.4
Za Minica	1	68.5	68.5	68.5	0	.	.	.	1	170.0	170.0	170.0	0	.	.	.	1	5.1	5.1	5.1	1	3.4	3.4	3.4
P. antiquus	24	77.0	60.0	90.5	8	221.1	190.6	253.6	8	190.4	153.4	256.9	5	479.2	382.9	552.2	24	4.8	3.8	6.9	20	2.6	2.1	3.1
L. atlantica	2	88.1	79.2	97.0	2	162.8	150.5	175.0	0	.	.	.	2	422.4	415.6	429.3	2	3.9	3.9	3.9	2	4.1	3.6	4.5
M. meridionalis	26	96.3	76.5	115.0	7	124.8	109.5	142.9	0	.	.	.	11	286.5	247.7	308.6	24	4.8	3.6	6.1	22	3.2	1.9	4.0
P. iolensis	3	104.7	96.0	114.0	3	179.3	153.4	198.0	0	.	.	.	0	.	.	.	3	3.9	3.4	4.7	3	3.1	2.4	3.4

Table 4.30. Mean, minimum and maximum values for lower M3 size-corrected indices. Min. is minimum, Max. is maximum, HI is hypsodonty index.

	Width (mm)				Hypsodonty Index				Min. HI				Length Index				Lamellar Frequency				Enamel Index			
	n	Mean	Min	Max	n	Mean	Min	Max	n	Mean	Min	Max	n	Mean	Min	Max	n	Mean	Min	Max	n	Mean	Min	Max
Luparello 1	7	26.3	22.9	27.4	5	236.8	218.2	260.8	2	246.3	233.8	258.8	5	372.2	324.3	430.2	7	12.3	11.1	13.7	7	5.1	4.2	6.4
Spinagallo Cave	8	30.2	26.6	35.7	4	227.9	201.2	260.0	3	211.2	154.1	261.9	0	.	.	.	8	9.7	7.6	10.8	8	5.5	4.5	6.7
P. cypriotes	3	32.6	30.7	35.4	3	197.1	187.3	205.2	0	.	.	.	2	277.5	272.2	282.8	4	11.8	10.8	12.4	3	3.7	3.5	3.8
Malta 1	3	34.5	32.5	36.0	1	204.8	204.8	204.8	2	177.2	170.0	184.4	0	.	.	.	2	10.8	10.7	11.0	3	3.8	3.4	4.0
Luparello 2	3	43.6	40.0	47.5	3	223.2	189.2	272.9	0	.	.	.	2	352.2	347.1	357.3	4	9.0	7.7	10.3	2	3.4	3.1	3.7
Malta 2	9	49.0	42.2	53.3	2	210.8	208.5	213.1	5	215.4	198.5	229.4	5	345.3	332.0	357.6	8	8.1	7.1	9.4	9	3.1	2.8	3.7
P. tiliensis	1	49.1	49.1	49.1	0	.	.	.	0	.	.	.	0	.	.	.	1	8.1	8.1	8.1	1	3.2	3.2	3.2
Cavern di Carini	3	59.3	56.5	63.5	1	219.5	219.5	219.5	0	.	.	.	1	348.4	348.4	348.4	2	6.9	6.5	7.2	3	3.1	2.8	3.5
Ghar Dalam	3	65.3	58.0	76.0	3	229.2	210.5	238.6	0	.	.	.	0	.	.	.	6	7.3	6.6	8.2	3	3.0	2.7	3.2
Puntali Cave	19	65.7	58.5	78.5	7	221.9	204.7	250.0	5	210.0	193.2	224.0	3	338.3	325.0	361.2	25	7.0	4.8	8.0	19	2.9	2.4	3.4
Za Minica	2	66.3	64.5	68.0	2	226.7	217.6	235.7	0	.	.	.	0	.	.	.	2	6.6	6.5	6.8	1	3.1	3.1	3.1
P. antiquus	22	80.1	69.0	92.0	11	219.9	200.0	248.7	7	211.2	164.8	251.1	6	351.6	295.5	392.2	26	6.2	5.4	7.4	17	2.3	2.0	3.0
L. atlantica	2	87.0	84.7	89.3	1	172.6	172.6	172.6	0	.	.	.	2	332.4	297.6	367.1	2	4.4	4.3	4.4	2	3.5	3.2	3.8
M. meridionalis	34	97.4	74.0	121.5	19	133.1	104.5	158.1	0	.	.	.	17	267.5	218.9	297.7	33	5.4	4.5	6.4	29	3.1	2.1	3.8
P. iolensis	3	105.3	98.9	113.0	3	190.8	176.9	209.6	0	.	.	.	3	265.6	247.7	292.3	3	5.3	4.8	6.0	3	2.7	1.9	3.1

Table 4.31. Mean, minimum and maximum values for upper M3 size-corrected indices. Min. is minimum, Max. is maximum, HI is hypsodonty index.

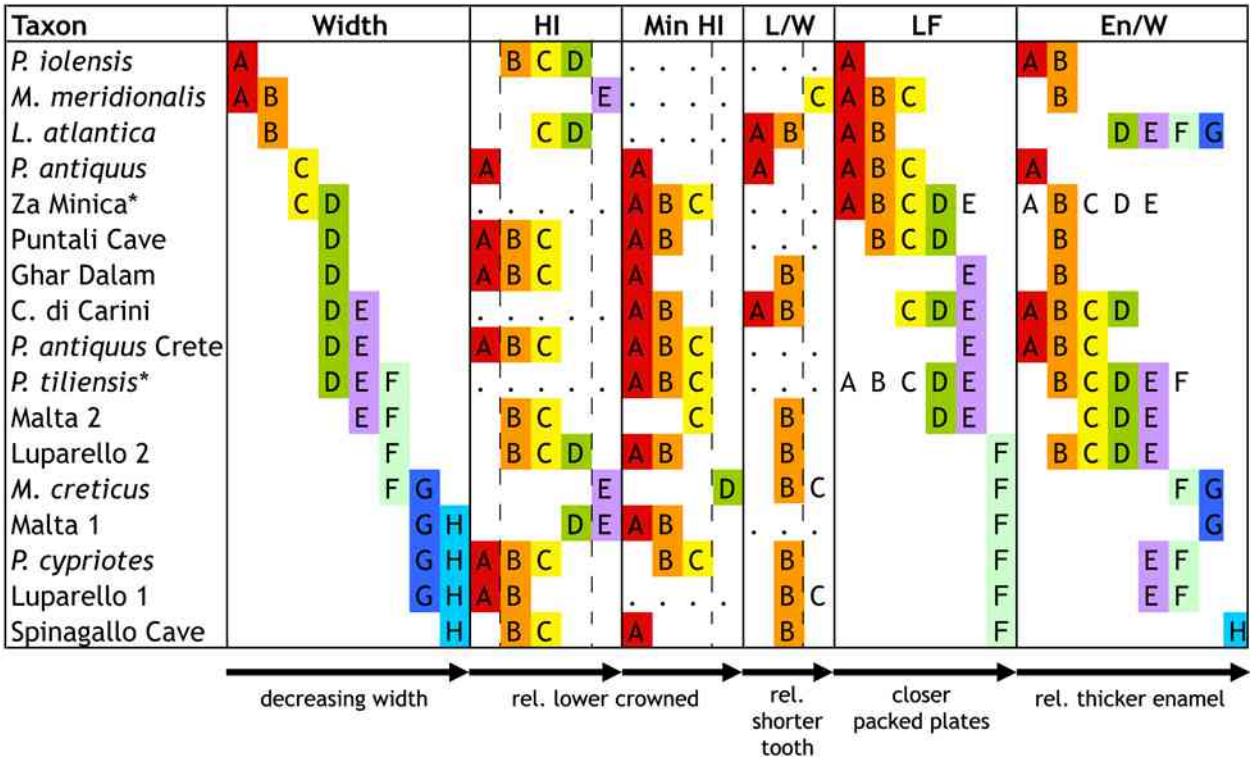

Figure 4.23. Summary of pair-wise comparisons (t-test; p<0.05) between mean values of lower M3 width and size-corrected indices. Taxa/OTUs are ordered from top to bottom by decreasing molar width. OTUs joined by the same letter/colour are not significantly different for that parameter. Taxa linked by an unshaded letter are not significantly different, but it is likely that non-significance results from low sample size (n=1) in that taxon rather than true similarity. Arrows indicate the morphological trends across groupings. Hypsodonty Index (HI), Minimum HI and Length Index (L/W) show no evidence of a size-related signal. Instead, shape differences between dwarf and full-sized elephants may provide evidence of different mainland sister taxa (dashed lines separate sample based on differences between full-size mainland taxa). Malta 1 groups with both *Palaeoloxodon* and *Mammuthus* for HI, but Min. HI values suggest HI scores underestimate the true range. Lamellar Frequency (LF) and Enamel Index (En/W) groupings indicate these traits show a size-related trend, although correspondence with width-based groupings is not exact.

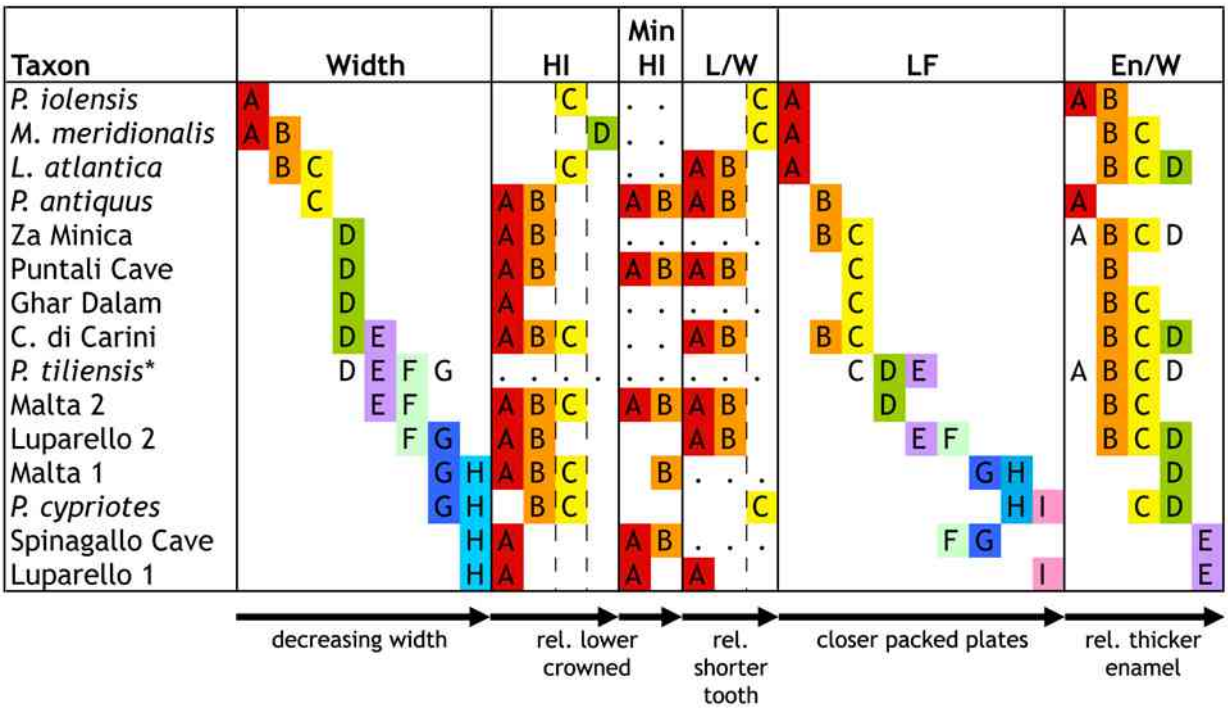

Figure 4.24. Summary of pair-wise comparisons (t-test; p<0.05) between mean values of upper M3 width and size-corrected indices. Abbreviations and figure explanation as Figure 4.29. As with lower M3s, HI, Minimum HI and Length Index (L/W) show no evidence of a size-related signal, suggesting tooth shape may reflect mainland ancestry (dashed lines). HI broadly groups all dwarfs into a 'high-crowned' group, with all except *P. cypriotes* grouping with *P. antiquus*. All dwarf mOTUs overlap with the *P. antiquus* HI range (Figure 4.31b). Length Index shows *P. cypriotes* to have relatively shorter teeth than dwarfs of equivalent size, similar to *P. iolensis* and *M. meridionalis*. Lamellar Frequency (LF) and Enamel Index (En/W) show a size-related trend, although correspondence with width-based groupings is not exact: smaller molars have closer-packed plates and relatively thicker enamel. *L. atlantica* appears slightly more similar to dwarf taxa, but this is not at odds with a size-related trend (unlike lower M3 Enamel Index).

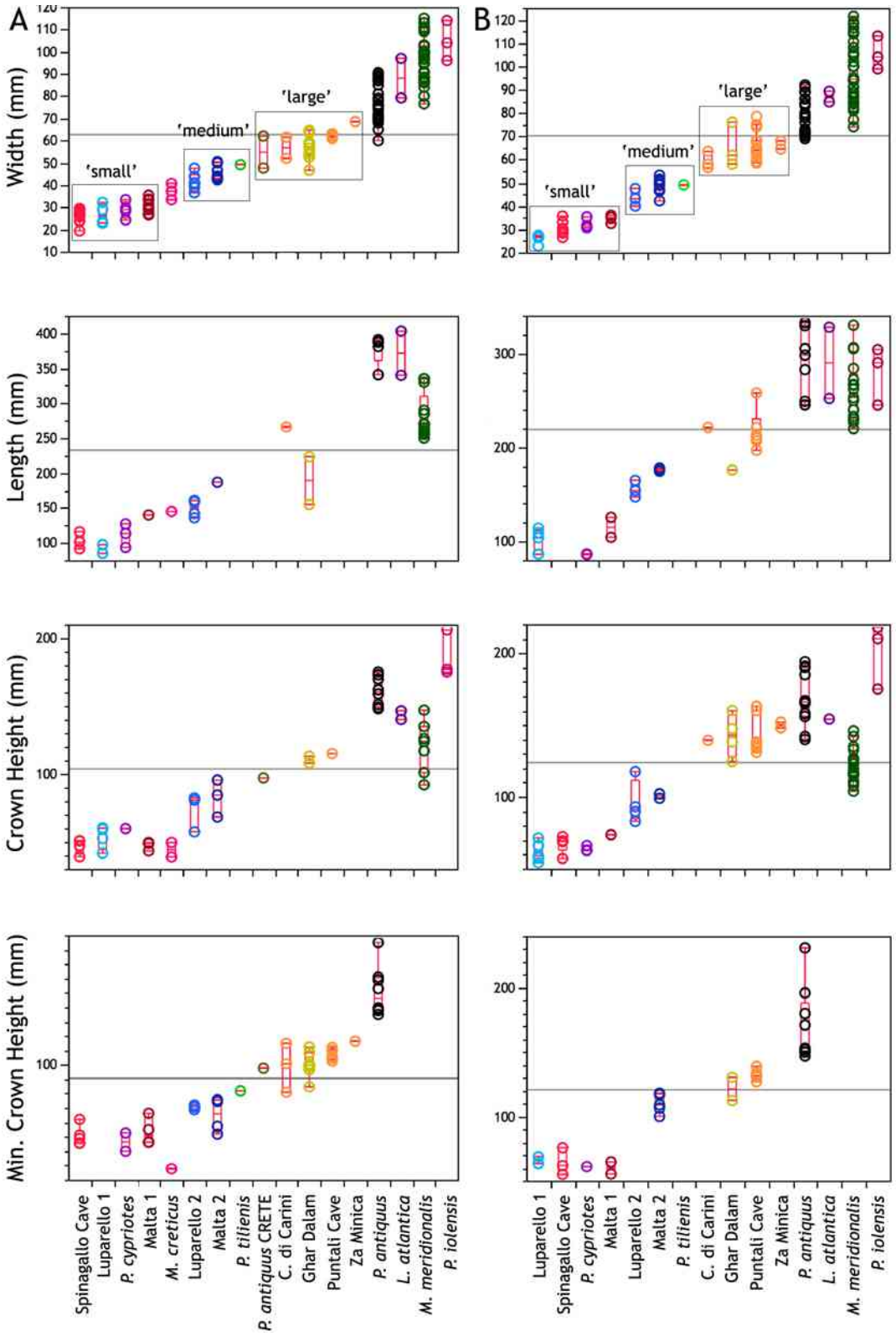

Figure 4.25. Box-plots of [A] lower and [B] upper M3 width, length and crown height for all dwarf mOTUs and full-sized taxa included in this study. Taxa are arrayed from left to right on the basis of mean molar width. Dwarf mOTUs are divided into three broad size-classes on the basis of molar width ('small', 'medium' and 'large'; see text); mOTUs of the same size-class also overlap in molar length and crown height, and cannot be separated from each other on the basis of any proxy of molar size. Differences in size between full-sized taxa can be used in conjunction with shape indices (Figure 4.26) for taxonomic discrimination, whereas shape alone is useful when making comparisons with dwarf taxa.

based on the inclusion of M9384 and the identity of this smaller-sized molar is not confirmed as M3 (see above). Each of these size-classes enables the comparison of trends between dwarf elephant populations known to be phyletically independent (Western vs Eastern Mediterranean), a key requirement for identifying evolutionary parallelism in dental evolution. Dwarf mOTUs in the same size-class also overlap in M3 length and height (Figure 4.25), indicating that mOTUs group similarly on the basis of all proxies for molar size and that size alone is undiagnostic.

Indices of dental variables were calculated for upper and lower M3s of dwarf mOTUs and full-sized elephant taxa (Tables 4.30 & 4.31). Pair-wise comparisons of mean values for tooth shape indices (Hypsodonty and Length Indices) produced no size-related trends (Figures 4.26 & 4.27; equivalent to isometric change): taxa of varying size were largely indistinguishable from one another, and differences (e.g. in *M. creticus* HI) are potentially linked to mainland ancestry (discussed below). Lamellar Frequency (LF) and Enamel Index (EI) show a size-related (allometric) trend, although correspondence with width-based groupings is not exact (lower and upper molars, Figures 4.23 & 4.24): smaller molars have closer-packed plates and relatively thicker enamel and, within each size-class, Eastern Mediterranean mOTUs fall within the range of variation of Western Mediterranean mOTUs. (Figures 4.26 & 4.27).

L. atlantica has relatively thick enamel in comparison to other full-sized taxa, particularly evident in lower M3 analysis, which may reflect closer taxonomic affinity with the smaller dwarf taxa (see below). A size-related trend is not undermined by this possibility; Figure 4.27 clearly shows smaller dwarfs to have relatively thick enamel, regardless of which mainland species is hypothesized to be sister-taxon/ancestor to those dwarfs.

Lamellar Frequency and Enamel Index appear to increase in variability in smaller dwarf taxa (Figure 4.26). This may reflect the disproportionate affect of measurement error at small absolutes sizes (especially in enamel thickness), or signify greater 'real' variability in the smaller dwarf taxa. LF shows a number of outliers to the general size- related trend in uppers and lower M3s from Spinagallo Cave and Luparello 1, indicating variability in these taxa is higher than expected (Figure 4.27). The most extreme upper M3 outlier, CU 278 from Spinagallo Cave, fits the trend in lower M3s, suggesting this specimen was wrongly identified as an upper molar. Re-examination of specimen notes and pictures show that although the wear surface is slightly concave (indicating lower), this could be the result of post-mortem damage. Its plates are parallel and straight, and its roots are angled anteriorly (indicating upper). Hypsodonty index sheds no further light, as CU 278 is worn into the paired-root region of the tooth. Based on the root and plate morphology, re-classifying this tooth as lower to fit the prevailing LF trend seems inappropriate; the low LF of this tooth and the two lower M3 may instead relate to the region of the tooth LF was taken on. All three outlying specimens are either anterior or posterior fragments, and plate frequencies in these regions are often considered 'abnormal' (Lister pers. comm.). As small-sized dwarfs have low plate counts and much shorter teeth,

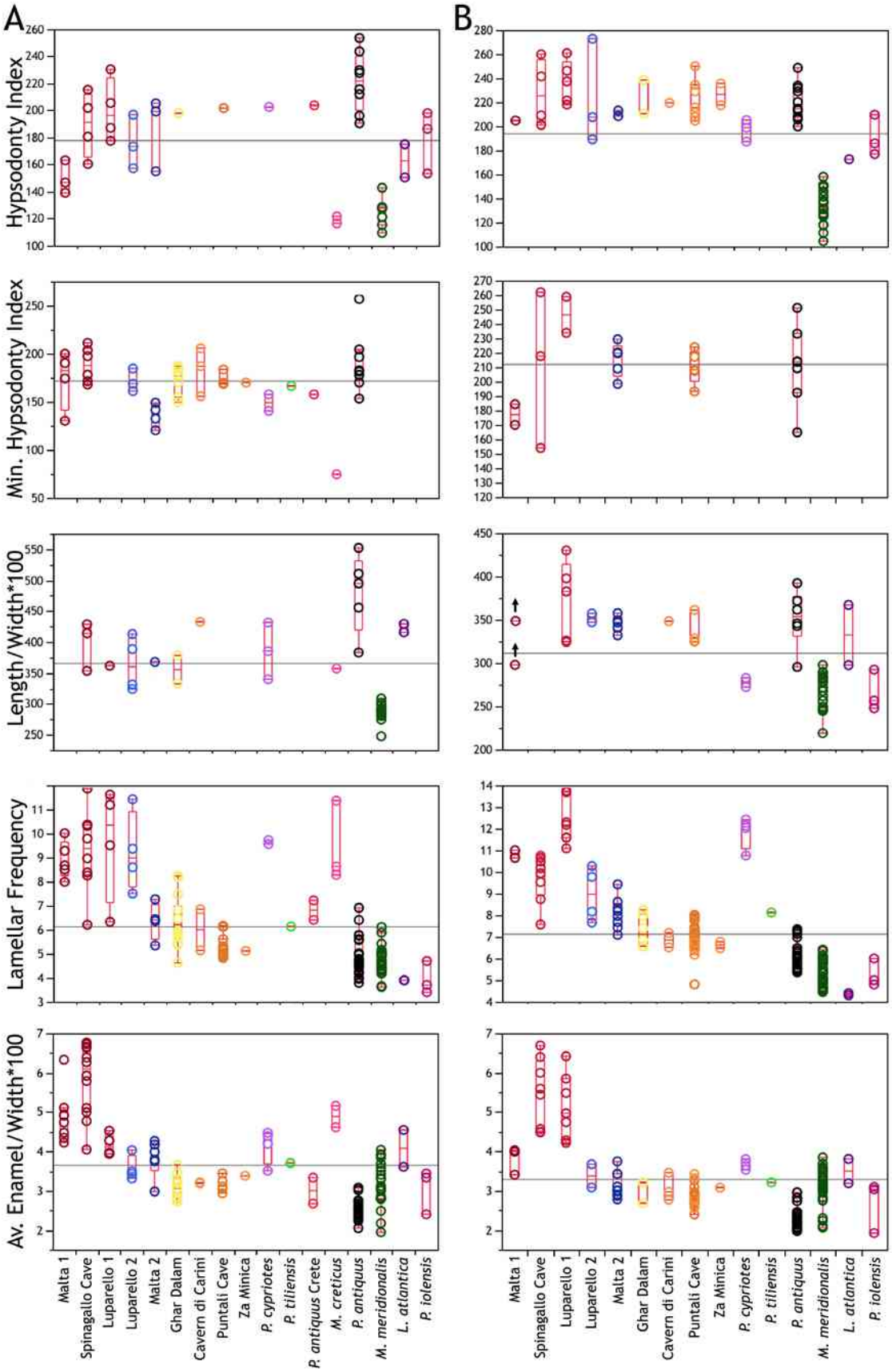

Figure 4.26. Box-plots of size-corrected indices of [A] lower and [B] upper M3s in dwarf elephant mOTUs and full-sized mainland elephants. mOTUs that can be grouped at a higher hierarchical level have the same point colour. Box-plot details in Figure 4.9. Malta 1 specimens are included for upper M3 Length Index, despite being underestimates, to enable qualitative comparisons with other OTUs.

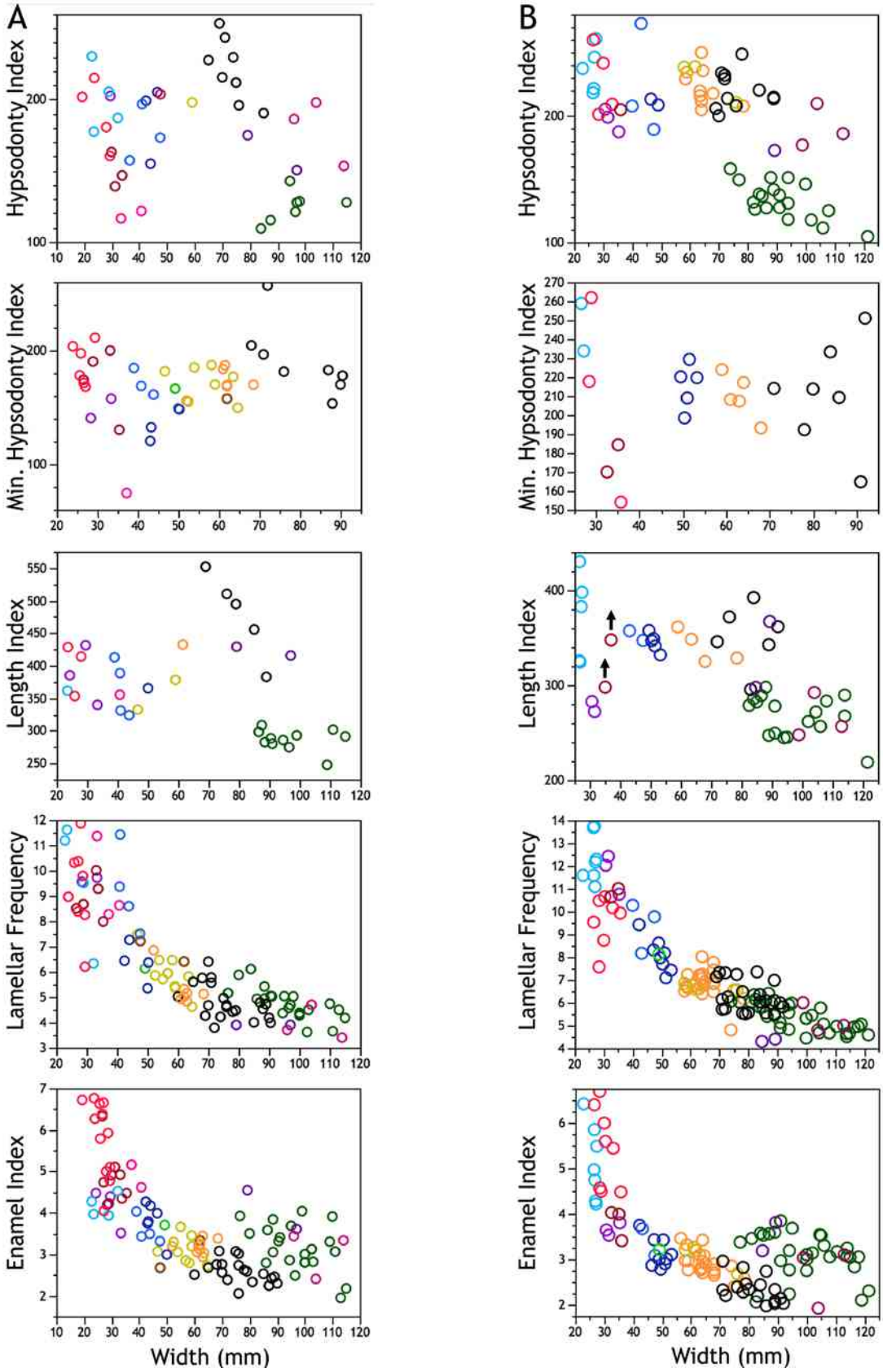

Figure 4.27. Scatter-plots of size-corrected indices against molar width. A. Lower M3, **B.** Upper M3. Light red, Spinagallo Cave; turquoise, Luparello 1; dark red, Malta 1; light purple, *P. cypriotes*; light pink, *M. creticus*; light blue, Luparello 2; dark blue, Malta 2; light green, Tilos; yellow, Ghar Dalam; brown, *P. antiquus* CRETE; orange, Sicily 3; black, *P. antiquus*; dark green, *M. meridionalis*; dark purple, *L. atlantica*; dark pink, *P. iolensis*.

inclusion of this 'abnormal' variation may further explain the higher LF variation in small taxa: one is more likely to sample within these regions.

Enamel Index is plotted against M3 width, its denominator (Figure 4.27), the negative curve could thus be an artefact of this as it would be expected even if there was no correlation between M3 width and enamel thickness. There is, however, a negative correlation between enamel thickness and molar width (Chapter 6), and significant differences between mOTUs in mean enamel thickness, despite % ME (Figures 4.16-4.19 for verification in a subset of dwarf and full size data). Enamel Index also shows a similar trend when plotted against other proxies for tooth size (length and crown height; not shown) and thus this size-related trend is not artefactual

Qualitative dental characters

As mOTU mean molar width increases, the frequency of lightly folded and highly folded enamel also tends to increase (Figure 4.22; character states 1 (red) and 2 (green), respectively). Similarly, and perhaps linked, larger taxa tend to have a higher frequency of secondary expansions and are less likely to lack medial expansions, although this relationship is less precise (Figure 4.22). *P. cypriotes* is unique as the only dwarf mOTU to entirely lack medial expansions in both upper and lower M3s, although its level of enamel folding is similar to mOTUs of equivalent size. Enamel figure shape and early wear patterns do not show size-related trends, and may better shed light on ancestry (see below): dwarf mOTUs of all sizes, with the exception of *M. creticus*, show similar character-state frequencies, and are also similar to *P. antiquus*. *M. creticus* differs to all other dwarf mOTUs in not exhibiting a lozenge shaped enamel figure (Ghar Dalam's variation in this trait is discussed above), and always showing an 'equal' early wear pattern (Figure 4.22). In addition, the medial expansions observed in *M. creticus* are (i) vestigial and (ii) appear to be 'looped', and may not be homologous to the triangular expansions observed in other dwarf taxa and *P. antiquus*. Sample sizes are small for both *P. cypriotes* and *M. creticus* (Tables 4.21 & 4.22; in consequence, early wear pattern could not be observed in *P. cypriotes* due to a lack of specimens at the appropriate wear stage), but these features have been confirmed in non-M3 teeth from the same site (pers. obs.).

Postcrania

Principal components analyses of shaft variables of the ulna (7 variables), humerus, femur and tibia (all 6 variables) enable a comparison of Sicilian mOTUs with *P. tiliensis*. For all four long-bones, eigenvalues for principal component one (PC1) summarize 96-98% of the total variation (Figure 4.28), indicating differences between mOTU limb bones relate primarily to size and size-related (allometric) shape. Humerus (Figure 4.28A) and tibia (Figure 4.28D) eigenvector loadings are approximately equal for all variables, and PC1 is an axis of isometric change in these bones (isometric value (I) = $1/\sqrt{p}$, where p is the number of variables included in the analysis (Jolicoeur 1963); $I_{6\ var.}$ = 0.4082). Ulna eigenvectors for DL, MDML, MDAP and DAP also approximate isometric change

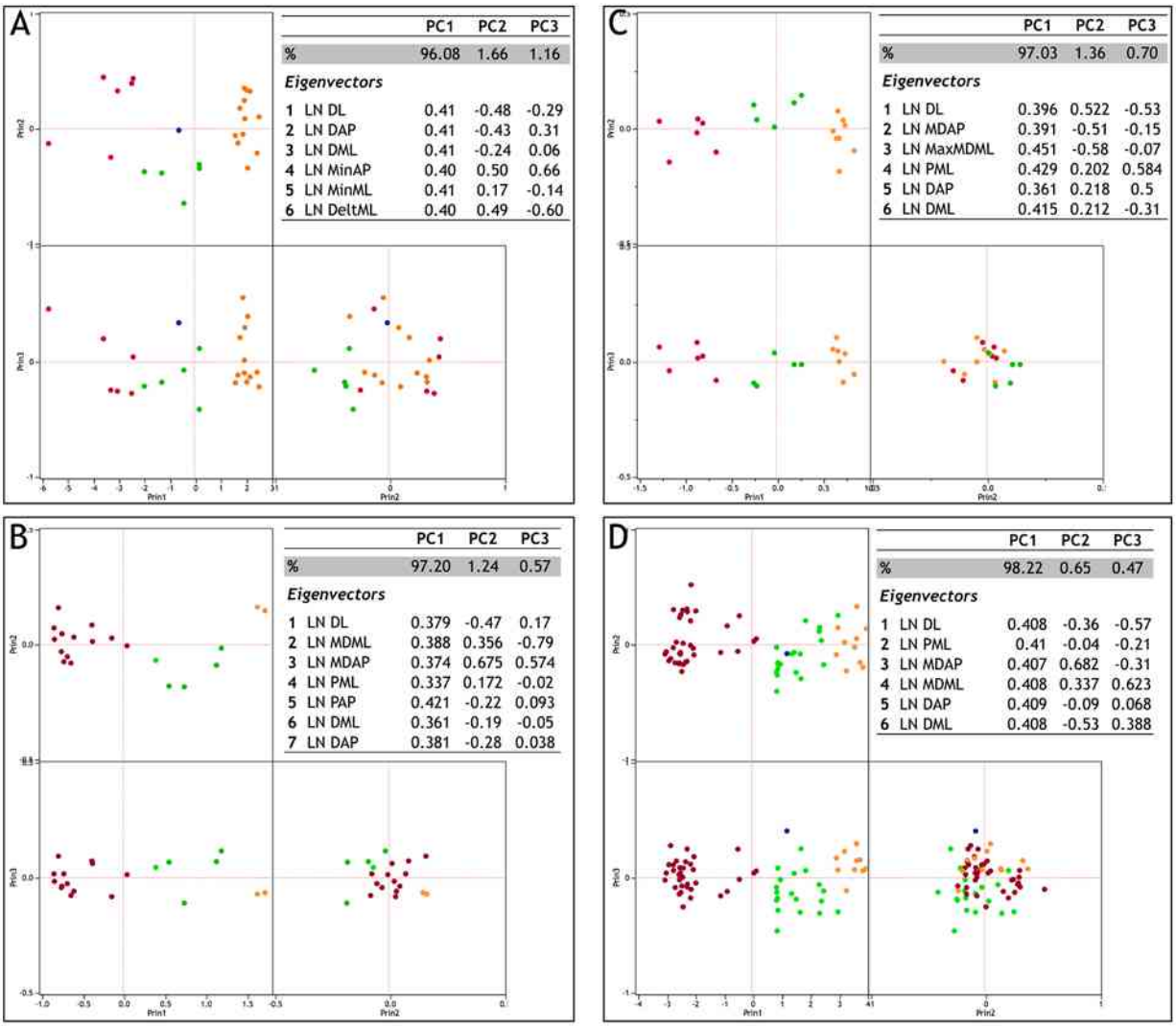

Figure 4.28. Principal components analyses of dwarf elephant long-bones. A. Humerus, **B.** Ulna, **C.** Femur, **D.** Tibia. In all analyses, principal component (Prin.) 1 explains almost all of the variation observed among dwarf elephants, indicating that size and size-related (allometric) shape variation explains the majority of differences among populations. Tilos and Sicilian dwarf elephants separate along PC2 or PCs 2 & 3 for all long-bones. Inset tables provide eigenvector scores and PC loadings for each analysis. Red points are Spinagallo Cave, green points are Tilos, orange points are Sicily 3 and blue points are Luparello Cave. Measurement abbreviations as in Table 4.3.

(Figure 4.28B; $I_{7\ var.} = 0.3780$), whereas PAP shows positive allometry (eigenvector loading > I) and PML and DML show negative allometry (eigenvector loading < I). Femur eigenvector loadings indicate weak negative allometry in DL and MDAP, weak positive allometry in DML, strong negative allometry in DAP and strong positive allometry in MaxMDML and PML (Figure 4.28C).

Despite describing only a small proportion of the total variability, PC2 and PC3 do suggest a shape difference between Tilos and Sicilian elephants not explicable by size. *P. tiliensis* separates from Sicilian elephants along both PC2 and PC3 axes in the humerus and tibia, both of which were isometric for PC1, although separation is less clear in the tibia (Figure 4.28 A&D). In the humerus, the same two variables have the highest eigenvector loadings for PC2 and PC3: MinAP and DeltML (DL is also highly loaded on PC2). In the tibia, eigenvector loadings for PC2 are highest on MDAP and DML; on PC3 MDML and DL have the highest loadings. The femur and ulna show separation along PC2 only (Figure 4.28 B&C), with the highest eigenvector loadings on shaft lengths and midshaft diameters in both bones.

Plotting femur distal AP against femur ML further indicates that (i) there appears to be a common bivariate trend for all dwarf taxa and (ii) mOTUs of similar size, but independent evolutionary origin, cannot be distinguished from one-another (Figure 4.29). *P. cypriotes* falls within the 95% confidence ellipse of Spinagallo Cave, and the 95% confidence ellipse of *P. tiliensis* encompasses *P. mnaidriensis* material as well as overlapping with the smaller Sicily 3 material.

Impact of homoplasy

Allometric trends are investigated further in Chapter 6, but this preliminary analyses indicates that size is the major diagnostic for dwarf elephant M3s and post-crania: (i) mOTUs of the same size-classes (based on width) cannot be discriminated from one another on the basis of other univariate tooth size proxies (length and crown height), (ii) teeth of the same size will also be similar in LF, relative enamel thickness and enamel folding and (iii) long-bones of similar size will be also be similar in overall shape (although there does appear to be subtle difference between Sicilian and Tilos elephants). Parameter variables that do not show size-related trends (HIs, LI, enamel figure and, possibly, the absence of medial expansions) may reflect relationships at a higher taxonomic level, providing evidence for probable ancestry (see below), although these effects are difficult to distinguish without risk of circular reasoning. Taxa of the same size, with a common ancestor, are therefore likely to be phenetically indistinguishable, and the over-riding factor determining their discrimination has to be contextual: are they contemporaneous and sympatric? This raises the further issue of the level of spatio-temporal allopatry meriting taxonomic separation of mOTUs. When these data are lacking, it must be recognised that the phenetic groupings identified here may be polyphyletic, and contain multiple taxa grouped on the basis of homoplasy.

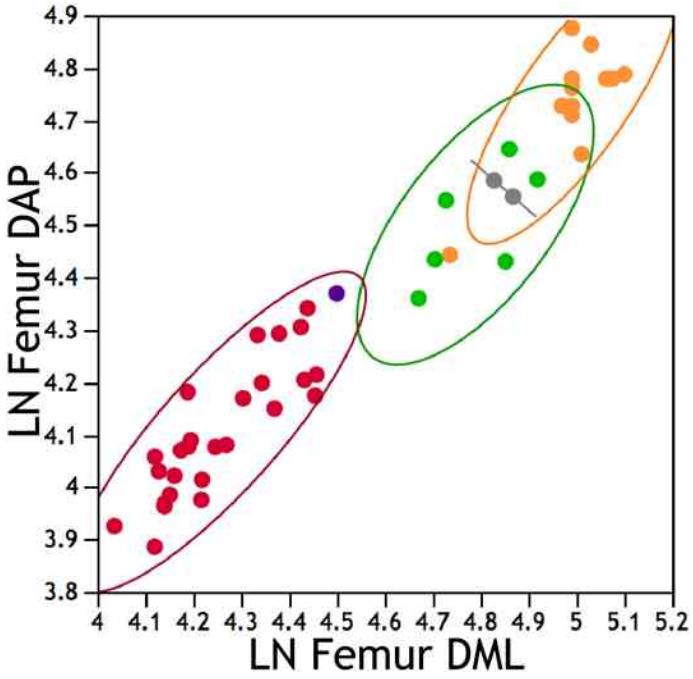

Figure 4.29. Scatter plot of dwarf elephant distal femur ML vs distal Femur AP with 95% confidence ellipses for dwarf elephant OTUs. Similar-sized dwarf elephants from different islands (phyletically independent dwarf lineages) are indistinguishable from each other: *P. cypriotes* (purple) falls within the 95% confidence ellipse of Spinagallo Cave elephant from Sicily (red). *P. mnaidriensis* from Malta (grey), and small (possibly female) Sicily 3 (orange) fall well within the 95% confidence ellipse and point scatter for Tilos elephants. There is also a tight correlation between all dwarf taxa indicative of a shared size-related trend (this is explored further in Chapter 6).

4.3.6. Generic affiliation of dwarf taxa

Dwarf elephant mOTUs were compared with *M. meridionalis*, *P. antiquus*, *P. iolensis* and *L. atlantica* for M3 size indices and qualitative dental characters (full-sized elephant taxa present in North African and Southern European Middle-Late Pleistocene faunas; *M. trogontherii* was not included due to time constraints, Maglio (1973) data for this taxon is restricted to summary measurements of questionable accuracy (Lister pers. comm.) Full-sized taxa can be differentiated on the basis of tooth shape (HI and LI used in conjunction), plate number (not shown), and tooth size (Figures 4.23-4.26): (i) *P. antiquus* has relatively narrow, higher crowned teeth, a plate count of 16-20, and is significantly different to the three other full-size elephants in HI (although overlap occurs with *P. iolensis* at the bottom end of its ranges); (ii) *P. iolensis* and *L. atlantica* cannot be differentiated on the basis of HI or plate count (13-17 and 12-15 respectively), and show an intermediate level of hypsodonty between *P. antiquus* and *M. meridionalis*, but do differentiate in absolute size (*P. iolensis* is wider and higher crowned than *L. atlantica*, Figure 4.25); (iii) upper M3 LI differentiates between *L. atlantica* and *P. iolensis* (Figure 4.26), along with molar width and length (Figure 4.25; there is no lower M3 length data for *P. iolensis*); (iv) molar size and LI (upper and lower M3s) cannot, however differentiate between *L. atlantica* and *P. antiquus*; (v) LI does not discriminate between *M. meridionalis* and *P. iolensis* (Figure 4.26), and nor do absolute values of molar width or length (Figure 4.25); they can be separated on the basis of crown height as (vi) *M. meridionalis* has (both relatively and absolutely) low crowned teeth, distinct from the other three species, but its plate count (11-14) cannot delineate it from *P. iolensis* or *L. atlantica* (Figure 4.25). In addition *L. atlantica* has relatively thick lower M3 enamel, but overlaps in range with *M. meridionalis* for both upper and lower M3 EI, and is not significantly different from *P. iolensis* in upper M3 EI (Figure 4.26). Although absolute size difference can inform taxonomic discrimination among mainland taxa, shape differences must take precedence when trying to establish higher level (e.g. genus) taxonomic relationships between dwarf and full-sized taxa.

Qualitative dental characters cannot differentiate between *P. antiquus*, *P. iolensis* and *L. atlantica* (Table 4.23): all have lozenge-shaped enamel figures, with medial expansions, lightly-highly folded enamel, and a short-long-short early wear pattern. Medial expansions are weak or absent in *M. meridionalis* (Maglio 1973), and unfolded to lightly folded enamel; most diagnostically, relative to *P. antiquus*, *P. iolensis* and *L. atlantica*, *M. meridionalis* enamel figures have parallel sides, sometimes expanding to form a sub-circular medial region, and in early wear form equal-sized enamel rings or a sub-circular medial ring between two elongated rings. Using these qualitative characters to infer sister-taxon relationships for dwarf elephants is limited, and can be no more specific than *M. meridionalis*-like or *Palaeoloxodon/L. atlantica*-like.

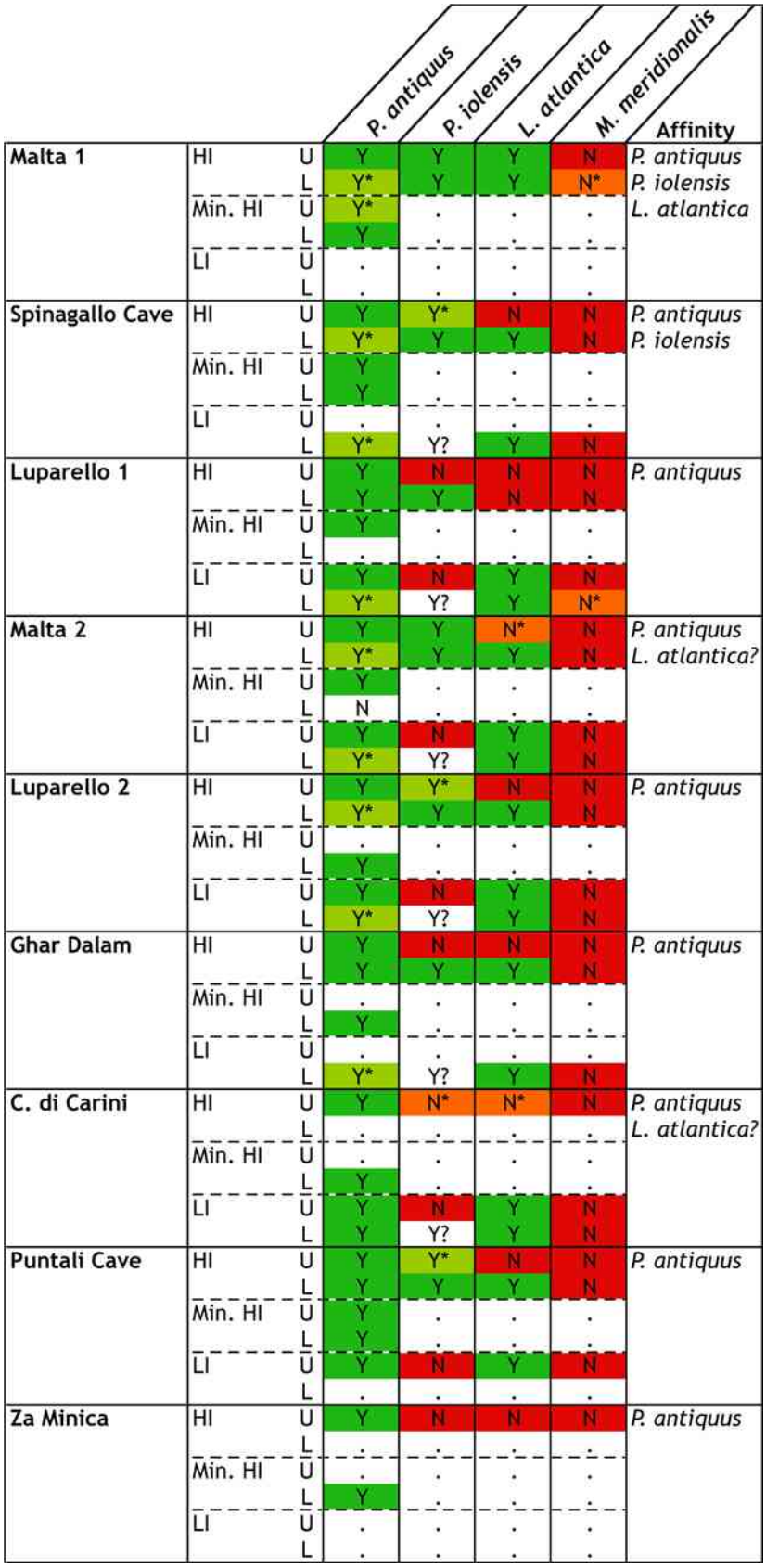

Table 4.32. Putative affinity of Sicilian and Maltese dwarf mOTUs with full-sized mainland taxa based on M3 shape. Legend overleaf.

Sicilian and Maltese elephants

Generic affiliation with *M. meridionalis* can be rejected for all Maltese and Sicilian mOTUs: (i) mean HI and LI values for upper and lower M3s are significantly different from, and do not overlap with, *M. meridionalis*, with the exception of Malta 1 HI which is shown to be an underestimate of the true range when lower M3 Min. HI is considered (Figure 4.26; Tables 4.30 & 4.32), and (ii) on the basis of qualitative characters (early wear and enamel figures), which instead support a *Palaeoloxodon/L. atlantica* relationship for dwarf mOTUs (Table 4.23).

Establishing the affinity of dwarf mOTUs within the *Palaeoloxodon/L. atlantica* group on the basis of tooth shape is problematic, due to small sample sizes and missing data, as well as conflicting signals from upper and lower molars, and from LIs and HIs (Tables 4.32 & 4.33). Mean lower M3 LI is significantly different between *P. antiquus* and all Sicilian or Maltese mOTUs except C. di Carini, suggesting that generic affinity should be rejected (Figure 4.23). However, there is considerable overlap between dwarf mOTUs and *P. antiquus* ranges (Figure 4.25). Significant differences for this parameter also reject *P. iolensis* affinity (but not *L. atlantica*) for most taxa, yet dwarf ranges encompass both African full-sized taxa (Figure 4.25). Four dwarf mOTUs also show affinity with either *P. iolensis* or *L. atlantica*, or both (Malta 1, Spinagallo Cave, Malta 2 and C. di Carini; Table 4.32), but as upper M3 LI comparisons (the basis for rejecting *P. iolensis* affinity in other mOTUs) were not possible for these mOTUs this should be treated with caution.

The combined evidence therefore provides the strongest support for generic attribution to *Palaeoloxodon* for all Sicilian and Maltese mOTUs, with *P. antiquus* as their sister taxa/putative ancestor (Table 4.32). This may, however, need to be revised in light of more *L. atlantica* data. If *P. antiquus* is the sister taxon of Sicilian and Maltese dwarf elephants, a reduction in relative molar length and, to a lesser extent, relative crown height, appears to have occurred in lower M3s (explored further in Chapter 6).

Crete

Palaeoloxodon/L. atlantica affinity is rejected for *M. creticus* on the basis of qualitative dental characters (absence of both lozenge-shaped enamel figures and a short-long-short early wear pattern (Table 4.23), and tooth shape (lower M3, all indices; Table 4.33). Instead, *M. creticus* shares a sub-equal early wear pattern and parallel-sided enamel figure with sub-circular medial region with *M. meridionalis* (Table 4.23). Affinity with *M. meridionalis* is also supported by HI, with *M. creticus* lower M3s relatively lower crowned than all other dwarf elephant mOTUs (Figures 4.23 & 4.26). Lower M3 LI indicates *M. creticus* is relatively longer than *M. meridionalis*, and more similar to other dwarf elephant mOTUs (Figure 4.26). Although this difference is non-significant (Figure 4.23, n=1 for *M. creticus*), it potentially undermines a case for *M. meridionalis* ancestry. Allometric trends implicated in the dwarfing process may, however, accommodate these shape differences (Chapter 6), and inclusion of *M. creticus* in the genus *Mammuthus*, with *M. meridionalis* as sister-taxon/putative

Table 4.32. Putative affinity of Sicilian and Maltese dwarf mOTUs with full-sized mainland taxa based on M3 shape. Combining t-test (Figures 4.23 & 4.24) and range (i.e. overlap; Tables 4.30 & 4.31, Figure 4.30) information to assess similarity between dwarf and full-sized elephants: **Y** (green), samples are not significantly different and ranges overlap; **Y*** (light green), samples are significantly different but ranges either overlap or (if n=1 for either sample) fall at the edge of each other's range; **N** (red), samples are significantly different and ranges do not overlap; **N*** (orange), samples are non-significantly different but (if n=1) there is a large disjunction between samples, or overlap probably results from underestimated dwarf mOTU measures; **Y?**, samples possibly overlap and/or are not significantly different based on estimated LI (used solely for *P. iolensis*, see text). Potential affinity is rejected if any index is scored as N. N* suggests affinity is less probable, but should not be rejected (species affinity qualified by ?). Affinity is accepted if all indices score Y or Y*. U is upper, L is lower.

			P. antiquus	*P. iolensis*	*L. atlantica*	*M. meridionalis*	Affinity
M. creticus	HI	U	.	.	.	.	*M. meridionalis?*
		L	N	N	N	Y	
	Min. HI	U	.	.	.	.	
		L	N	N	N	.	
	LI	U	.	.	.	.	
		L	N	Y?	N*	N*	
P. antiquus CRETE	HI	U	.	.	.	.	*P. antiquus*
		L	Y	Y*	N*	N	*P. iolensis?*
	Min. HI	U	.	.	.	.	*L. atlantica?*
		L	Y	.	.	.	
	LI	U	.	.	.	.	
		L	.	.	.	.	
P. cypriotes	HI	U	Y*	Y	Y*	N	*P. iolensis?*
		L	Y	Y	N*	N	
	Min. HI	U	.	.	.	.	
		L	Y	.	.	.	
	LI	U	N	Y	N	Y	
		L	Y*	Y?	Y	N	
P. tiliensis	HI	U	.	.	.	.	*P. antiquus*
		L	.	.	.	.	
	Min. HI	U	.	.	.	.	
		L	Y	.	.	.	
	LI	U	.	.	.	.	
		L	.	.	.	.	

Table 4.33. Putative affinity of Eastern Mediterranean dwarf mOTUs with full-sized mainland taxa based on M3 shape. Legend as Table 4.32.

ancestor is advocated.

Qualitative characters and HI support a *P. antiquus* affinity for *P. antiquus* Crete material, although affinity with *P. iolensis* and *L. atlantica* cannot be ruled out (Tables 4.23 & 4.33). Affinity with *M. meridionalis* is rejected on the basis of hypsodonty index (Table 4.33), enamel figure and early wear pattern (Table 4.23).

Cyprus

Affinity with *M. meridionalis*, and thus generic attribution to *Mammuthus*, is rejected on the basis of (i) tooth shape (Table 4.33) and (ii) the presence of lozenge-shaped enamel figures (Table 4.23). Early wear pattern was not scorable for *P. cypriotes*, and consequently shared character states for enamel figure shape provide the only qualitative character support for affinity with *Palaeoloxodon*/L. atlantica. *P. cypriotes* is unique among all dwarf mOTUs in completely lacking medial expansions in upper and lower M3s. Medial expansions are also sometimes absent in other dwarf taxa, limiting their use as a diagnostic tool and suggesting that the loss of this character may be related to the dwarfing process. Taxonomic significance should not, however, be ruled out.

Tooth shape rejects affinity with both *P. antiquus* and *L. atlantica*: *P. cypriotes* appears to have relatively shorter upper M3s (Figure 4.26, Table 4.33). In contrast, lower M3 LI is similar to other dwarf mOTUs and overlaps with *P. antiquus, L. atlantica* and *P. iolensis.* Affinity with *P. iolensis* is not rejected, but there are no lower M3 LI data for this taxa. Using tooth LF and an estimated plate count of 16 from Maglio (1973), a lower M3 LI range for *P. iolensis* can be estimated as 330-490 (reconstructed length estimate = plate count/LF*100), which would show considerable overlap with *P. antiquus*, *L. atlantica* and all dwarf mOTUs, and thus be consistent with a *P. iolensis*-*P. cypriotes* affinity (indicated as Y? in Table 4.33). The attribution of *P. cypriotes* to the genus *Palaeoloxodon* is thus supported, with *P. iolensis* as its most likely sister-taxon.

Tilos

Qualitative dental characters support *Palaeoloxodon/L. atlantica* affinity for *P. tiliensis* (enamel figure and early wear pattern, Table 4.23), and reject *M. meridionalis* affinity. Tooth shape can only be compared with *P. antiquus* (Min. HI, Table 4.33), and does not reject affinity with this taxon. However, as comparisons cannot be made, affinity with the *P. iolensis* and *L. atlantica* cannot be rejected. In consequence, inclusion of *P. tiliensis* within the genus *Palaeoloxodon* is recommended, but comparisons with additional full-sized taxa are need for sister-taxon identification to be systematically robust.

4.4. Discussion

4.4.1. Genus-level revision

The generic attribution of dwarf taxa is often taken as an explicit statement of putative mainland ancestry. However, North African Pleistocene elephant taxa are rarely included in discussion of dwarf elephant systematics, in part because the taxonomy of these full-size taxa is convoluted and the subject of ongoing debate (Todd 2005, 2010). In consequence, taxonomic debate is simplified and polarized as a choice between *Palaeoloxodon* or *Mammuthus*, with just two species (*P. antiquus* and *M. meridionalis*) considered as likely sister taxa. Inclusion of two North African Pleistocene species in this study highlights the need for further work, both in regard to dwarf elephant ancestry and to elephantid systematics in general (e.g. the similarities between North African *L. atlantica* and *Palaeoloxodon*). Similarities in dental morphology between *Palaeoloxodon* and *L. atlantica* are clear, suggesting revision of this taxon is required. Osborn (1942) placed the co-type of *L. atlantica* in *Palaeoloxodon,* and recent cladistic analyses identify *L. atlantica* as sister-taxon to *P. recki recki*, within a predominantly palaeoloxodontine clade (Todd 2005, 2010). *L. atlantica* is described as having a *Loxodonta*-like skull (a key diagnostic trait; Maglio 1973). As it is (i) unclear if this skull material is from North or South African *L. atlantica*, between which there are other morphological differences, and (ii) no skull material appears to have been described for *P. iolensis* for comparison, generic attribution of either taxon may be questionable.

P. iolensis and *L. atlantica* data were taken from Maglio (1973), and interpretation and conclusions are thus limited by unknown intra-observer error between my data, Maglio's data and Lister and Van Essen's data, issues of data comparability and quality (some of Maglio's data is considered problematic, Lister pers. comm.), as well as small sample size. Despite this, similarities in tooth shape and in qualitative dental characters between North African full-size elephants and Mediterranean dwarf taxa are clear, and robust rejection of either as sister-taxa will require additional data.

Generic attribution in this study is based on (i) the presence of diagnostic dental characters and (ii) phenetic similarity in tooth shape, and does not employ cladistic methodology. A preliminary cladistic analysis of dwarf mOTUs and full sized taxa dental characters (Appendix 7) produced 1273 most parsimonious trees, collapsing to an unresolved polytomy for in-group taxa in the strict consensus tree. Additional characters and a detailed consideration of character coding and character variability are necessary for a meaningful cladistic analysis of dwarf elephant systematics, and is beyond the scope of this thesis.

Qualitative dental characters can only reject *Mammuthus* affinity, so that if *Mammuthus* is rejected, tooth shape indices alone must be used to assess putative sister-taxa relationships with full-

sized taxa. Given the possibility of allometric change (Chapter 6), using a similarity criterion of this kind may result in erroneous conclusions. For example, *P. antiquus* ancestry for Sicilian and Maltese elephants would suggest that insular dwarfing is accompanied by a reduction in relative tooth length: all Sicilian and Maltese dwarf mOTUs included are more similar to each other and to *L. atlantica* for this index, although there is overlap with *P. antiquus*. *L. atlantica* ancestry would require a relative increase in crown height, raising the question of whether a reduction in relative tooth length is of less taxonomic importance than an increase in relative crown height during insular dwarfism. To mediate this issue, I take the conservative view that taxonomic revision should only be made if current attribution can be rejected, emphasizing nomenclatural stability, whilst discussing the implications of morphological difference. Despite the limitations of a non-cladistic approach for inferring higher level taxonomic relationships, and acknowledging the preliminary nature of my conclusions, this study shows clear similarities between dwarf and full-size taxa that are likely to have systematic importance.

***Palaeoloxodon* is retained for Sicilian and Maltese taxa**

The current attribution of Sicilian and Maltese dwarf elephant taxa to *Palaeoloxodon*, with *P. antiquus* as sister-taxon/mainland ancestor, cannot be rejected on the basis of dental characteristics. Mol *et al.* (1996) and Poulakakis *et al.* (2006) suggested that material attributed to *P. falconeri* should be revised to *Mammuthus* on the basis of its antiquity; this is refuted for all Maltese and Sicilian taxa on the basis of morphological evidence. However, similarities with *L. atlantica* are clear, and may merit further investigation: (i) Malta 1 and Malta 2 appear relatively lower crowned than Sicilian taxa in the same size-class, (ii) upper M3 HI (the index responsible for rejecting affinity with *L. atlantica* in most mOTUs) in *L. atlantica* is based on a single specimen and could represent the bottom end of the range in that taxon, and (iii) relatively thick enamel in *L. atlantica* could support an affinity with the smaller dwarf taxa (particularly with Spinagallo Cave, which appears to have relatively thick enamel even in relation to the general allometric trend). In addition, cladistic analysis (Todd 2005, 2010) placed *P. mnaidriensis* (= Malta 2) as sister-taxon to a (*L. atlantica*, *P. recki recki*) clade, although the overall topology of these cladograms are at odds with the consensus view of elephantid inter-relationships (e.g. *Loxodonta*, *Elephas* and *Mammuthus* are all paraphyletic in her study), and no node support values are provided.

A brief consideration of material not included in this study (due to time constraints and ongoing research by other scientists) provides further support for generic attribution to *Palaeoloxodon*. *L. atlantica* affinity can be excluded for Puntali Cave material: Puntali Cave skulls show the developed parietal-occipital crest and parietal bosses characteristic of *Palaeoloxodon* (Ferretti 2008), whereas *L. atlantica* has a typical *Loxodonta*-like skull (Maglio 1973). This argument cannot be extended to other Sicily 3 mOTUs which lack cranial material (Za Minica and C. di Carini), and support for their inclusion in *Palaeoloxodon* rests entirely on dental characteristics and their presumed conspecificity

with Puntali Cave material (see below).

Cranial material from Spinagallo Cave assemblage cannot reject *L. atlantica* affinity: whilst they lack key *Palaeoloxodon* cranial characters such as the parietal-occipital crest, Spinagallo Cave skull morphology has been shown to be paedomorphic (Accordi & Palombo 1971), and broad similarities between *E. maximus*, *L. africana* and *P. antiquus* juvenile crania make taxonomic discrimination difficult (Palombo 2003). Palombo (2003) notes three *L. africana*-like features (low orbit position, position of external choanae and a relatively large forehead) in Spinagallo Cave material, as well as *Palaeoloxodon*-like flared premaxillaries. Evidence for generic affiliation is therefore equivocal. However, no quantitative, comparative study of skull ontogeny among the Elephantidae has been carried out and no direct comparison with *L. atlantica* cranial material has been made. Furthermore, derived *Palaeoloxodon* cranial features such as the parietal-occipital crest are thought to develop late in ontogeny (Ferretti 2008). It is therefore difficult to evaluate the significance of absence or presence of cranial characters in the light of current knowledge and evidence.

Loxodonta affinity is also challenged for Malta 1/Malta 2. A fragment of stylohyoid from Benghisa Gap is figured in Adams (1874); the wide angle between the inferior ramus and the posterior ramus ('angle y' in Shoshani *et al.* 2007) and relative posterior ramus (PR) length do not support *Loxodonta* affinity (PR is broken, but is longer than the superior ramus (SR) and thus reconstructed PR length must result in an SR:PR ratio of less than 1). However, the taxonomic usefulness of this specimen is questionable: (i) stylohyoid autapomorphies for *P. antiquus* and *L. atlantica* have not been established (and thus synapopmorphies for *Loxodonta* rest on a single taxon, *L. africana*; Shoshani *et al.* 2007), (ii) the Benghisa Gap stylohyoid is not associated with dental material and mOTU attribution cannot be made (both Malta 1 and Malta 2 are present at this site) and (iii) phylogenetic relationships within the Elephantidae based on hyoid characters are controversial (Shoshani *et al.* 2007, p.181). Morphological assessment of the stylohyoid from Malta is also preliminary and qualitative, and a more in depth study is needed.

Maglio (1973) notes that *L. atlantica* enamel figure shows 'bifurcated, y-shaped' medial expansions, a possible autapomorphy for this taxon. I was unable to verify this character state in *L. atlantica* in accompanying plates, but where medial expansions are present in Sicilian and Maltese material, they do not correspond to this description. Instead they are either triangular and distinct, and similar to *P. antiquus*, or a vestigial point, or absent. There is no clear pattern (related to size or to mOTU) of the frequency of these character states (hence both vestigial and triangular expansions were coded as 'present'), suggesting intraspecific variability is common. Thus, whilst the absence of a putative *L. atlantica* autapomorphy provides no support for a sister-taxon relationship between *L. atlantica* and Maltese or Sicilian dwarf taxa, the variability of medial expansion character states in dwarf mOTUs suggest that this character may have limited taxonomic utility in dwarf elephants.

Palaeoloxodon* is retained for *P. cypriotes

The current attribution of *P. cypriotes* to *Palaeoloxodon* is retained, but upper M3 shape suggests that *P. iolensis* is its most likely sister-taxon, challenging the consensus view that *P. cypriotes* descends from *P. antiquus* (e.g. Vaufrey 1929, Osborn 1942, Davies 2002, Palombo 2001a). However, Middle-Eastern Middle Pleistocene elephants have not been included in this or previous studies, and are poorly-known. Taxonomic revision of Turkish material may provide evidence for geographic variation in *P. antiquus,* or the presence of other possible ancestral taxa, that could accommodate the shape differences seen in *P. cypriotes* upper M3s (Ebru Albayrak, pers. comm.). Previous work on European *P. antiquus* showed little evidence of geographical or temporal patterns in dental morphology (Davies 2002), but – as with this study – the sample was heavily biased towards German and British specimens, and comparisons with southern European material (e.g. Italy or Greece) have not been made. Furthermore, this rejection rests entirely on upper M3 length index, and upper M3 lengths are more prone to underestimation than lower M3s owing to the angle of eruption. Ratios may also enhance small absolute differences in the constituent parameters. A comparison of the raw length and width data for *P. cypriotes* indicates it overlaps with the Sicilian and Maltese 'small-sized' elephants for both variables, and that shape differences in *P. cypriotes* may be exaggerated. Similarly, *P. cypriotes* does not deviate significantly from the wider isometric trend, and shares ontogenetic similarities with *P. antiquus* (see Chapter 6). The data is not suffiecient to rule out a sister-taxon relationship with *P. antiquus*,.

If *P. iolensis* were established as the sister-taxon of *P. cypriotes*, this would impact on the degree of dwarfism recorded in this taxon: *P. iolensis* has wider, higher crowned M3s than *P. antiquus*, and *P. cypriotes* M3s are closer to 30% of *P. iolensis* values versus being approximately 40% of *P. antiquus* values. Reconstructed lower M3 lengths for *P. iolensis* (based on Maglio's estimated plate count of 16 and LF values from Maglio (1973)) range from 340-471mm, overlapping with *P. antiquus* and *L. atlantica* values, in line with the similarity of upper M3 measures in these taxa. Percentage size change in *P. cypriotes* on the basis of tooth length is thus the same regardless of the putative sister-taxon employed. *P. cypriotes* mean length, width and crown height as percentages of *P. iolensis* values show a similar size reduction signal across all three tooth-size proxies, further supporting affinity with this taxon (i.e. tooth shape change as defined by the three key variables length, height and width can be inferred to be approximately isometric).

The absence of medial expansions in all *P. cypriotes* specimens is unique among Mediterranean dwarf elephants (if not diagnostic, as other dwarf mOTUs include some specimens which lack medial expansions), and whilst enamel simplification appears to accompany size reduction, this may reflect taxonomic affinity with a mainland elephant taxa not included in this analysis. For example, *M. trogontherii* lacks medial expansions, and is broadly similar to *P. antiquus* in tooth shape (often resulting in taxonomic confusion of these taxa). However, the lozenge-shaped enamel figures of *P. cypriotes* preclude affinity with *M. trogontherii*. Again, the relative taxonomic importance of

characters underpins taxonomic decision: if *M. trogontherii* were shown to be similar in molar shape to *P. cypriotes* (or, for that matter other Mediterranean dwarf taxa), would enamel figure shape be considered more informative than the presence or absence of medial expansions? Early wear pattern could not be scored for *P. cypriotes* M3s; CT scanning of unworn plates would allow this character to be scored, and is a focus of future work. A more detailed analysis of the variation in all characters between and among elephant taxa, the use of cladistic methodology to investigate homoplasy and identify genus level diagnostic characters, and a consideration of the factors that control molar morphology are all needed to address these issues. On the basis of this study, however, inclusion of *P. cypriotes* in the genus *Mammuthus* is not supported, and taxonomic affinity with *M. meridionalis*, a possibility suggested by Bate (1904, 1905), is rejected.

M. creticus* is confirmed as *Mammuthus

Poulakakis *et al.* (2006) proposed the revision of *'E (P)'. creticus* to *Mammuthus* on the basis of aDNA evidence. The credibility of their results have, however, been called in to question (Binladen *et al.* 2007, Orlando *et al.* 2007) due to 'serious theoretical and methodological flaws' (Binladen *et al.* 2007, p.56), and debate continues regarding the generic attribution of *M. creticus*. Previous morphological similarity between *M. creticus* and *M. meridionalis* was noted by Bate (1907) and Mol *et al.* (1996), with the latter suggesting revision of *'E. (P.)' creticus* to *Mammuthus* on the basis of this (unquantified) similarity and the antiquity of the *M. creticus* material. I have challenged the consensus view that *M. creticus* material is older than 800,000 years old, and the validity of using its antiquity to justify generic revision (sections 3.4.2 & 4.1.1). This study provides morphological evidence for *Mammuthus* affinity, and rejects attribution to *Palaeoloxodon*, independent of disputed aDNA and geochronological evidence.

Early wear pattern and enamel figure morphology in *M. creticus* are diagnostic for *Mammuthus*, and relative crown height suggests that *M. meridionalis* is its likely sister-taxon. Relative tooth length in lower M3s is more similar to other dwarf elephants than to *M. meridionalis*, challenging a sister group relationship. Although the *M. meridionalis* sample is highly limited in geographical range (a single locality, Val d'Arno), it is a good indication of the true range of lower M3 length variation in this taxa (A. Lister, pers. comm). *M. creticus* has a similar LI to other 'small' and 'medium' sized dwarf elephants, the size classes it groups with on the basis of tooth width, which suggests a potential size-related signal that is explored further in Chapter 6.

If *M. meridionalis* and *M. creticus* are sister-taxa, shape differences require allometric change in teeth during the dwarfing process. This questions the validity of a 'similarity' criterion for ascertaining taxonomic affinity, and thus tooth shape alone may not be enough to identify sister-taxa (with implications for *P. cypriotes* and Sicilian and Maltese taxa). Qualitative characters reject *Palaeoloxodon* affinity for *M. creticus*, and also support *Mammuthus* affinity, and thus revision of *M. creticus* to *Mammuthus* is robust to any such issues with tooth shape (and, additionally, allometric

trends can accommodate *M. meridionalis* as sister-taxon; Chapter 6).

Confirmation of *Mammuthus* affinity for *M. creticus* cannot, however, be used in support of Poulakakis *et al.* (2006). *Mammuthus* identity has been established independently of aDNA and geochronological evidence and thus cannot validate the proposed antiquity of the sample or the credibility of aDNA results. The lack of diagnosibility of the rib-fragment used by them for aDNA analysis, the incongruence between the described 'cave' locality of this specimen and my observations of the Cape Maleka region (section 3.4.2, Appendix A1.3.1), and the refutation of the purported mammoth aDNA autapomorphies by Orlando *et al.* (2006) and Binladen *et al.* (2006), mean any connection between Poulakakis *et al.'s* material and the *M. creticus* hypodigm is tenuous. Furthermore, the 800,000 year old antiquity of *M. creticus* cannot be supported by current evidence (Chapter 3). Even if the rib fragment can be shown to belong to *M. creticus* on the basis of further analysis and the veracity of amplified aDNA from that fragment confirmed, the additional claim that this is one of the oldest amplified aDNA remains unsupported. The debate over the validity of Poulakakis *et al.* (2006) remains unresolved. In contrast, resolution of the taxonomic debate is achieved by an independent line of morphological evidence presented in this study. *M. creticus* is a mammoth, intermediate in size to the small-sized and medium-sized dwarf *Palaeoloxodon*. In fact, by comparing *M. creticus* with literature data for other dwarf mammoths (Table 4.34) it can be seen that *M. creticus* is the smallest mammoth species ever to have lived, indicating that extreme insular dwarfism is seen in two Elephantidae genera.

Palaeoloxodon* is retained for *P. tiliensis

The current attribution of *P. tiliensis* to *Palaeoloxodon*, with *P. antiquus* as sister taxon, cannot be rejected, and no taxonomic revision is supported on the basis of current evidence. However, as (i) only limited *P. tiliensis* dental material was available and (ii) tooth-shape comparisons are limited to *P. antiquus*, further investigation is required. It should also be noted that sister-taxon affinity with *L. atlantica* and *P. iolensis* also cannot be rejected on the current evidence, and comparisons with Middle- Eastern elephant taxa have not been made. There is uncertainty as to the number of mainland genera present in the Tilos region during the Middle-Late Pleistocene, although there is currently no evidence for the presence of *Loxodonta* in this region (Ebru Albayrak, pers. comm.). Caution should thus be used when making explicit statements about ancestry or sister-taxa relationships for *P. tiliensis*.

Ancient DNA extracted from Tilos material is used to support a sister-taxon relationship between *Palaeoloxodon* and *Elephas* (Poulakakis *et al.* 2002b), and subsequent aDNA analysis places *P. tiliensis* within the *E. maximus* clade (Poulakakis *et al.* 2006), suggesting that *Palaeoloxodon* is not a valid genus and should be synonymized with *Elephas*. The morphological data presented here support the attribution of *P. tiliensis* to *Palaeoloxodon*, and thus the validity of using this taxon to investigate *Palaeoloxodon-Mammuthus-Elephas* (Elephantini, *sensu* Shoshani *et al.* 2007) affinity.

However, given the criticism of the methodology of Poulakakis *et al.* (2006), all taxonomic inference based upon their work should be treated with caution, and I recommend the continued use of *Palaeoloxodon* until there is good support for the paraphyly of *Palaeoloxodon* with respect to *Elephas*.

Species	Island	Upper/Lower M3	width	length	Reference
M. creticus	Crete	Lower	37-40.7	144	This study
M. exilis	Santa Rosa	Upper	-	189	Lister (1996)
M. primigenius	Wrangel	Upper	~63-72	260	Lister (1996)
M. lamamorae	Sardinia	Upper	69	-	Melis et al (2001)

Table 4.34. Size comparison of island dwarf mammoths. *M. creticus* lower M3s were compared with upper M3 literature data for other dwarf mammoth species (only upper M3 data were available). Upper M3s are generally shorter than lower M3s, thus size-differences are underestimated, and this is a conservative illustration of *M. creticus'* small size. Upper M3s are generally wider than lower M3s, exaggerating the size difference with *M. creticus*. However, it is unlikely that an *M. creticus* upper M3 would be 30 mm wider than the lower M3, the necessary size-discrepancy required to make *M. creticus* larger than *M. lamamorae*.

4.4.2. Species-level revision of dwarf taxa

M. creticus, *P. cypriotes* and *P. tiliensis* are all supported as valid species and no taxonomic revision is necessary at the species level. Inclusion of material from Cyprus and Crete was limited by financial, access and time constraints and, in consequence, this study's findings cannot be used to make island-wide generalizations. Referred material for *P. cypriotes,* as well as 'large-sized' elephant material, excavated from other Cypriot localities, needs to be compared with *P. cypriotes* material from Imbohary before the number of dwarf elephant taxa on Cyprus can be assessed with confidence. Similarly, while no other material (bar the rib fragment sampled by Poulakakis *et al.* (2006)) has been referred to *M. creticus*, the validity of *P. antiquus creutzburgi*, and thus the number of Cretan dwarf elephant taxa, cannot be assessed without the inclusion of the numerous specimens housed at Rethymnon Museum, Crete. However, this study represents the first effort to quantify and assess the taxonomic importance of variation in *M. creticus* and *P. cypriotes*, and supports the consensus view of the validity of these species.

***P. falconeri* and *P. melitensis* are synonymous**

Dwarf elephants on Sicily and Malta are currently referred to two species: *P. falconeri* and *P. mnaidriensis*. This study challenges the accepted taxonomy on three counts: (i) dental and postcranial material support the presence of at least three different-sized dwarf elephant taxa on Sicily and Malta, (ii) Sicilian material currently referred to *P. mnaidriensis* is not attributable to that taxon, and is a new species, and (iii) Luparello Cave material currently referred to *P. falconeri* does, in fact, comprise two different-sized elephant taxa corresponding to *P. falconeri* and *P. mnaidriensis*. Material from Ghar Dalam Cave, which has previously been only loosely incorporated into the existing taxonomic framework, is tentatively referred to the new species along with 'large-sized' Sicilian specimens but is considered problematic due to poor preservation. This study also highlights the nomenclatural issues surrounding *P. falconeri* and '*P. melitensis'* which have contributed to a misunderstanding of dwarf elephant taxonomy.

The common misconception that the three described dwarf taxa from Malta, *P. falconeri*, '*P. melitensis'* and *P. mnaidriensis*, represent three different size-classes corresponding to 'small', 'medium' and 'large', respectively, was refuted on the basis of the original published descriptions. Analysis of type-series data confirms this: there are only two differently-sized dwarf taxa identified from a combined sample of original *P. falconeri*, '*P. melitensis'* and *P. mnaidriensis* type and referred material. '*P. melitensis'* and *P. mnaidriensis* type-series and referred material each conform to a single species hypothesis, are distinct from one another in size, and are valid taxa. *P. falconeri* is a valid species name (section 4.1.1), but its type-series is entirely comprised of juvenile material and cannot be discriminated from either '*P. melitensis'* or *P. mnaidriensis*. *P. falconeri* is therefore a *nomen dubium* (Zoological Code article 75.5). There is no evidence for another 'small-sized' taxon on

Malta, in line with the observations by Adams (1874), however the presence of a third, 'large-sized' taxon on Malta is supported when Ghar Dalam material is included in the analysis. Thus, while there are three different-sized elephant taxa on Malta, these do not correspond to the described species, requiring synonymisation of two of the existing taxa, and the description of a new species.

Both Lydekker (1886) and Ambrosetti (1968) considered '*P. melitensis'* and *P. falconeri* to be synonymous; Busk (1867) indicated that there were greater similarities between '*P. melitensis'* and *P. falconeri* than between *P. falconeri* and *P. mnaidriensis*, and thus synonymy of the first two species better reflects the original author's species description, even if the type material is itself undiagnostic. Two molars (NHM 49239 and 49267), a femur (NHM 49260) and a humerus (NHM 49253) are included in the type-series for both '*P. melitensis'* and *P. falconeri* (Busk 1867; Falconer in Busk 1867, 1868). However, '*P. melitensis'* and *P. falconeri* are not objective synonyms (Zoological Code, article 61.3.4): Osborn (1942) fixed NHM 44312, an upper M3 molar that is not part of the *P. falconeri* type-series, as the lectotype for '*P. melitensis'*, rendering the rest of the '*P. melitensis'* type-series non name-bearing (NB. had this not occurred, *P. falconeri* and '*P. melitensis'* would be objective synonyms). I therefore concur with Lydekker (1886) and Ambrosetti (1968) that '*P. melitensis'* and *P. falconeri* are subjective synonyms.

Priority of '*P. melitensis'* over *P. falconeri* is likely: both species names were made available in the same publication (Busk 1867), but Lydekker (1886), as first reviser, synonymized them to '*E. melitensis*.' Currently, *P. falconeri* is widely used to refer to the smallest-sized dwarf elephant from Sicily and Malta, and '*P. melitensis'* has fallen out of general use. However, *contra* Ambrosetti (1968), criteria for the reversal of precedence set out in article 23.9 of the Zoological Code are not met: '*P. melitensis'* has been used as a valid name since 1899 (e.g. Osborn 1942), and thus prevailing usage cannot be used to argue for the reversal of precedence of *P. falconeri* over '*P. melitensis'*.

P. falconeri is, however, widely used for the 'small-sized' dwarf elephant material from Sicily. It would substantially undermine taxonomic stability and cause confusion amongst the wider researcher community if *P. falconeri sensu lato* (i.e. including the Sicilian material, see below) were synonymized to '*P. melitensis'*. *P. falconeri*, as a *nomen dubium*, requires the designation of a neotype. Given the observed morphological differences between Sicilian and Maltese 'small-sized' dwarfs (see below), and to preserve future taxonomic stability (Zoological Code, article 75.6), I advocate designation of a well preserved Spinagallo Cave skull (with associated teeth) as this neotype. Although this is at odds with the original type locality, it would fix the name *P. falconeri* with the site and material it is most associated with in the wider literature. In line with article 23.9.3 of the Zoological Code, this matter should be referred to the ICZN for ruling under its plenary power, recommending the conditional suppression of '*P. melitensis'* for the purposes of the Principal of Priority (article 81.2.3), and the designation of a *P. falconeri* neotype from Spinagallo Cave (article 75.6). Pending the submission of, and decision on, this application, the use of the junior synonym, *P.*

falconeri, should be maintained and applied to both *P. falconeri* and '*P. melitensis'* material from Malta (= Malta 1), as well as the 'small-sized' dwarf elephant material from Sicily (=Sicily 1).

Sicilian and Maltese small-sized mOTUs are referred to a single species

This study shows that the three 'small-sized' mOTUs from Sicily and Malta, currently referred to *P. falconeri*, are both significantly different from one another in a number of key dental variables, and that sample variation is, in part, at odds with a single-species hypothesis. CV evidence, in particular, suggests that Luparello 1 may be a separate dwarf taxon. However, sample overlap makes it impossible to accurately and consistently diagnose a specimen to the level of mOTU (Figure 4.20), and thus, despite these differences, I refer them to a single species of dwarf elephant, *P. falconeri*. Malta 1 is equivalent to the '*P. melitensis'* type-series; *P. falconeri* and '*P. melitensis'* are synonyms; Luparello 1 and Spinagallo Cave cannot be discriminated from Malta 1 to the extent that a differential diagnosis could be written (a requirement when describing a new species). This is a conservative taxonomic approach; the differences between each constituent mOTU certainly hint at a more complex evolutionary history and further evidence may show *P. falconeri* to be a meta-taxon, resulting in the splitting of this species. This is why I advocate only conditional suppression of '*P. melitensis*', and recommend a Spinagallo Cave specimen as the *P. falconeri* neotype.

<u>P. mnaidriensis</u> is a medium-sized taxon

Vaufrey (1929) and Osborn (1942) established the idea that *P. mnaidriensis* was a 'large-sized' dwarf elephant taxon, leading to the referral of Sicilian elephant material to this taxon based on relative size trends within that island. This study shows that, of the three different-sized dwarf elephant groups on Malta and Sicily, the name-bearing Maltese material is in fact a 'medium-sized' dwarf taxon. The only Sicilian mOTU that cannot be rejected as conspecific to Maltese *P. mnaidriensis* (=Malta 2) is Sicily 2 from Luparello Cave. This alters the usage of *P. mnaidriensis* for Sicilian taxa in two ways: (i) all Luparello Cave material is currently referred to *P. falconeri*; this study indicates that a subset of this sample should instead be referred to *P. mnaidriensis,* and (ii) the large-sized Sicilian material currently referred to *P. mnaidriensis* (e.g. that from Puntali Cave, Za Minica and San Teodoro Cave) should instead be referred to a new species. Thus, although these findings refute Vaufrey's (1929) classification of *P. mnaidriensis* as a 'large-sized' dwarf elephant, this study corroborates his observations of two, differently sized taxa at Luparello Cave. Like Vaufrey (1929) I attribute the smaller-sized taxon to *P. falconeri*, but attribute the larger, 'medium-sized' taxon to *P. mnaidriensis* (rather than *'P. melitensis'*).

This proposed revision has ramifications beyond elephant taxonomy. Currently, *P. mnaidriensis* lends its name to a Sicilian faunal complex, the '*P. mnaidriensis'* FC (section 3.4), based on the presence of 'large-sized' dwarf elephants that are here referred to a new species. Clearly it is nonsensical for this faunal complex to retain this eponymous title when *P. mnaidriensis* does not

form part of the constituent fauna, and it must be renamed. Given that the large-sized dwarf elephant is also thought to occur in a stratigraphically younger, and ecologically distinct fauna (Masini *et al.* 2008), and is therefore undiagnostic for this faunal complex, I recommend renaming it for either (i) a potentially diagnostic species such as *Hippopotamus pentlandi*, or (ii) a type-assemblage and/or stratigraphic layer. As this study demonstrates that faunal complex composition, by definition, is not robust to taxonomic revision, I strongly advocate the latter recommendation. This will also serve to underline the importance of faunal complexes as descriptive, rather than prescriptive, short-hand in palaeoecology, and caution against the over-reliance on faunal lists without due consideration of taxonomic reliability.

Linking taxonomy with geochronology and palaeogeography

Sicily was the only island of those included in this study for which geochronology and palaeogeography could potentially, albeit in a limited fashion, inform and/or impact on dwarf elephant taxonomy (section 3.5.1). Geochronological data indicated that the large-sized dwarf elephant material from Puntali Cave, San Teodoro Cave and Za Minica could not be temporally delineated from one another. This study shows that this material also cannot be taxonomically discriminated from one another, but can be discriminated for the geologically older Luparello and Spinagallo Cave material, confirming the geochronological independence of these sites. Puntali Cave, San Teodoro Cave and Za Minica material is thus referred to a separate species (*Palaeoloxodon* sp. nov.), that cannot be considered part of the same dwarfing lineage (i.e. is not ancestral to) Sicilian *P. falconeri*.

Geochronological evidence also indicated that there were two, stratigraphically distinct dwarf elephant taxa at Luparello Cave; this study confirms the presence of two taxa at this site. However, as the provenance of the material is unknown, we cannot be sure which of the two taxa is stratigraphically older. If it is the medium-sized dwarf elephant material (here referred to *P. mnaidriensis*), in line with Vaufrey's (1929) observations, then *P. mnaidriensis* could potentially be ancestral to *P. falconeri* (the taxon to which the small-sized material is referred; note, however, this observation may not be more broadly applicable – e.g. on Malta – given potential issues with Sicilian-Maltese synonymy).

Spinagallo and Luparello Cave material also could not be temporally discriminated, but these sites may have been situated on separate islands during the Early-Middle Pleistocene. While the material here is referred to a single taxon, *P. falconeri*, there is evidence of morphological differences that may indicate evolutionary independence, possibly owing to geographical isolation.

As *P. mnaidriensis* may have been ancestral to *P. falconeri*, there is only good evidence for at least five independent dwarfing events in *Palaeoloxodon,* and one in *Mammuthus* (Figure 4.30). However, if our interest is in the morphological correlates of insular body-size reduction, rather than the causes, or tempo and mode, of this evolution, we can partly circumvent the issue of discriminating

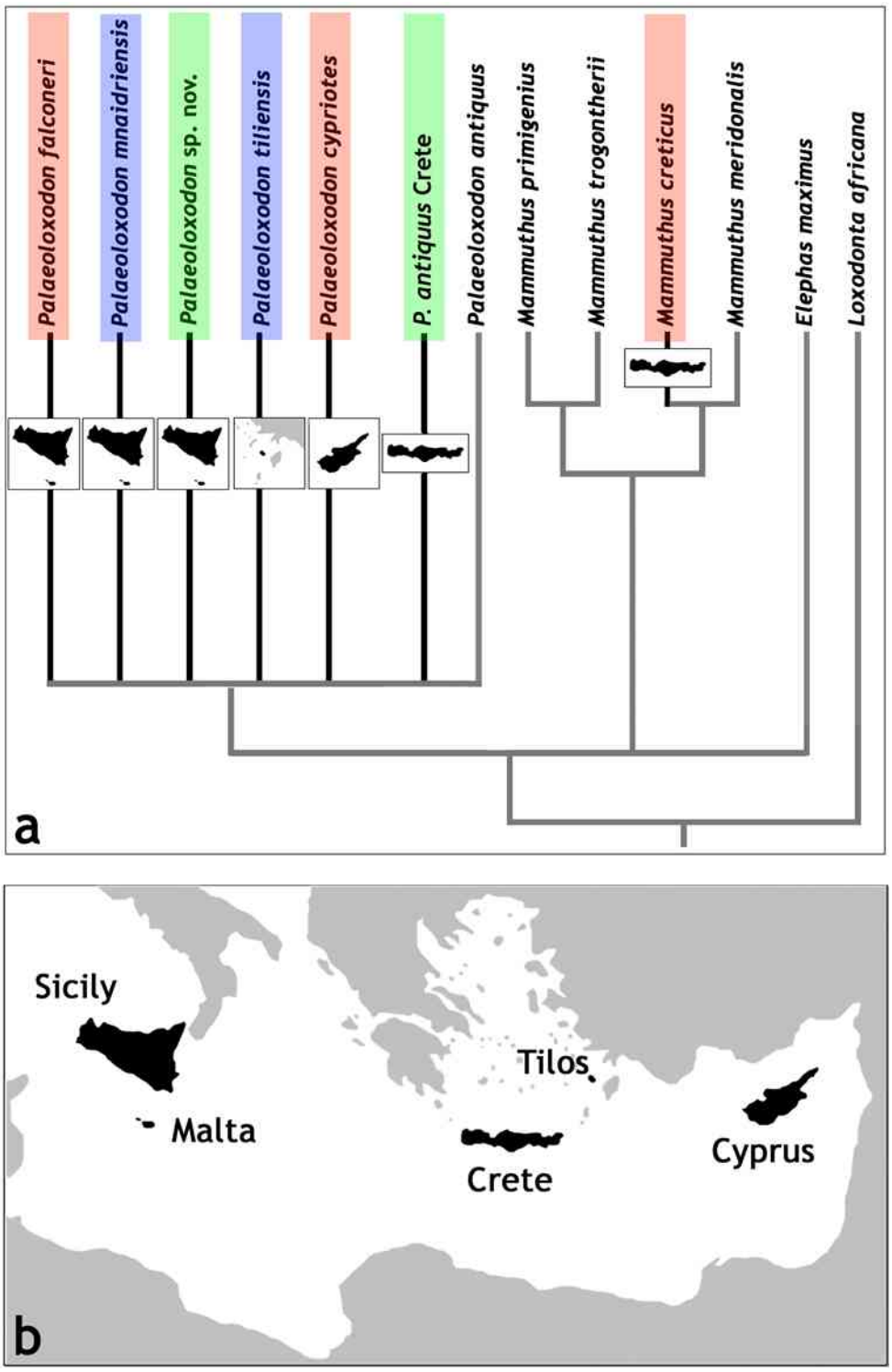

Figure 4.30. Mediterranean dwarf elephant inter-relationships and parallel evolution. [A] Proposed evolutionary relationships of dwarf elephants (black branches) with full-sized European Pleistocene elephants and extant taxa (grey branches); the evolution of 'small-sized' (red shading), 'medium-sized' (blue shading) and 'large-sized' (green shading) dwarfs occurred in parallel at least twice in *Palaeoloxodon*. A small-sized dwarf evolved at least once in *Mammuthus* (*M. lamamorae* was not included in this study and its generic affinity has not been validated). Sister-taxon relationships within *Palaeoloxodon* are difficult to establish, and thus dwarf taxa form a 'soft' polytomy with *P. antiquus* (shown), and *L. atlantica* and *P. iolensis* (not shown). **[B]** Map of the central and Eastern Mediterranean: islands included in this study shaded black.

individual lineages; each 'size-class' still represents an independent 'replicate' in a natural experiment of evolving to that body size. Thus, 'small-sized' dwarfs evolved at least three times in parallel in the Mediterranean, while 'medium-sized' and 'large-sized evolved at least twice (Figure 4.30).

The wider impact of homoplasy in dwarf elephant research

Comparisons of Eastern and Western Mediterranean dwarf elephant taxa show that similar-sized taxa are also indistinguishable in key taxonomic characters and overall morphology, highlighting the wider problem of homoplasy – and thus type II error – when identifying dwarf taxa. Even where shape differences are demonstrated, such as between *P. cypriotes* and the small-sized Sicilian and Maltese taxa, specimens fall within the 95% confidence ellipses of other, independently evolved dwarf taxa. This again stresses the possibility that Sicilian and Maltese species may be meta-taxa, liable to splitting if contextual evidence demonstrates geographic or temporal isolation. With this in mind, I recommend designating type material for the new, large-sized Sicilian dwarf taxa from a single site, Puntali Cave, ensuring that name-bearing material is geographically (and also probably temporally) constrained.

Given the variation among small-sized Sicilian and Maltese mOTUs, in particular, it is clear that an in-depth investigation of the palaeogeography and geochronology of these islands could shed considerable light on dwarf elephant evolution and taxonomy. Until such work has been carried out, the taxonomic recommendations of this study should not be seen, as the current supposed conspecifity of Maltese and Sicilian taxa is, as evidence for the contiguity of Malta and Sicily in the past, or as support for a common geochronological age. This argument can be extended to other Sicilian and Maltese endemic taxa which share the same geochronological ambiguities, as well as to endemic fauna from palaeo-archipelagos the world-over. Where parallel evolution is probable, endemic taxa cannot be used as biochronological markers with any degree of confidence.

Are dwarf elephant species good taxa?

This study has shown that distinct, phenetic groups of dwarf elephants can be identified and discriminated from one another, and these groups have been referred to separate species. However, whether these phenetic taxa do correspond to the rank of species remains a difficult question when dwarf elephant taxa are (i) recent, phyletic descendants of a contemporaneous mainland taxa and (ii) potentially undiagnosable without contextual evidence due to parallel evolution. The latter issue may reflect the limitations of morphological data in resolving closely related species; molecular characters (even if they are no longer available for sampling due to DNA degradation) may be able to establish good, monophyletic clades between or within islands. Establishing dwarf elephant species as distinct from their mainland ancestor is theoretically and practically more difficult to deal with.

It is clear that the very smallest dwarf elephant taxa cannot be classed as the same species as full-sized *P. antiquus* if a biological species concept is employed. *P. falconeri* and *P. cypriotes* are

approximately the same size as a neonate *L. africana* (see Chapter 6 for a discussion of body mass estimation), and mechanistic barriers to reproduction between those taxa and a 10,000kg ancestor are likely. This argument is of less use for larger dwarf taxa, and further difficulties arise given the incremental nature of size differences between phenetic groups. However, the data here shows that even the largest dwarf elephants on Sicily, Sicily 3, show limited overlap with, and are significantly different from, *P. antiquus* for dental and post-cranial parameters, and form a distinct phenetic cluster ($P<0.02$ for lower M3 plate count, width, LF and estimated crown height; upper M3 plate count, width, LF, crown height and estimated crown height; all long-bone shaft parameters). By these criteria, the large-sized dwarfs can be identified as distinct from *P. antiquus*, and appear to be a good palaeospecies. Arguably, all dwarf taxa could all be referred to sub-specific status, explicitly acknowledging ancestral origins and the potential paraphyly of the ancestral taxon if its dwarf descendants are excluded. The current ambiguity over the identity of mainland sister taxa precludes this and I support the validity of dwarf elephant taxa, as delineated here, as species, with the caveat that contextual evidence may later identify some of them as meta-taxa.

4.5. Conclusion

This chapter investigated the validity of the current taxonomic framework for Mediterranean dwarf elephants and has shown it to require substantial revision: 1. '*Elephas' creticus* should be referred to the genus *Mammuthus*; 2. Although Sicilian, Maltese, Cypriot, Tiliese and large-sized Cretan elephants remain in the genus *Palaeoloxodon*, sister-taxa relationships are hard to establish (Figure 4.30). With this caveat, I treat *P. antiquus* as their sister-taxon for the purposes of further investigation of allometric trends (Chapter 6): it is the best studied *Palaeoloxodon* species present in the Mediterranean region and is a 'good' taxon in its own right, minimizing the likelihood of introducing identification error; 3. At the species-level, this study upholds the validity and integrity of *P. tiliensis, M. creticus* and *P. cypriotes*; 4. '*P. melitensis'* and *P. falconeri* are synonymized to the junior synonym *P. falconeri* to maintain taxonomic stability; 5. *P. mnaidriensis* is shown to be a valid taxon, but the taxonomic integrity of its current hypodigm is disputed. Instead, the large-sized elephants from Sicily and Ghar Dalam Cave, Malta are referred to a new species (to be described elsewhere). This study also highlights the need for a systematic study of North African and Middle Eastern elephants, a pre-requisite for the identification of the mainland ancestors of Mediterranean dwarf elephants. Finally, dwarf elephant systematics is shown to be complicated by potential homoplasies relating to allometric change, and endemic species may in fact be meta-taxa. The parallel evolution of dwarf elephant morphology is explored further in Chapter 6.